

















**MADROÑO**  
A WEST AMERICAN JOURNAL OF BOTANY  
VOLUME XXXVI  
1989

**BOARD OF EDITORS**

**Class of:**

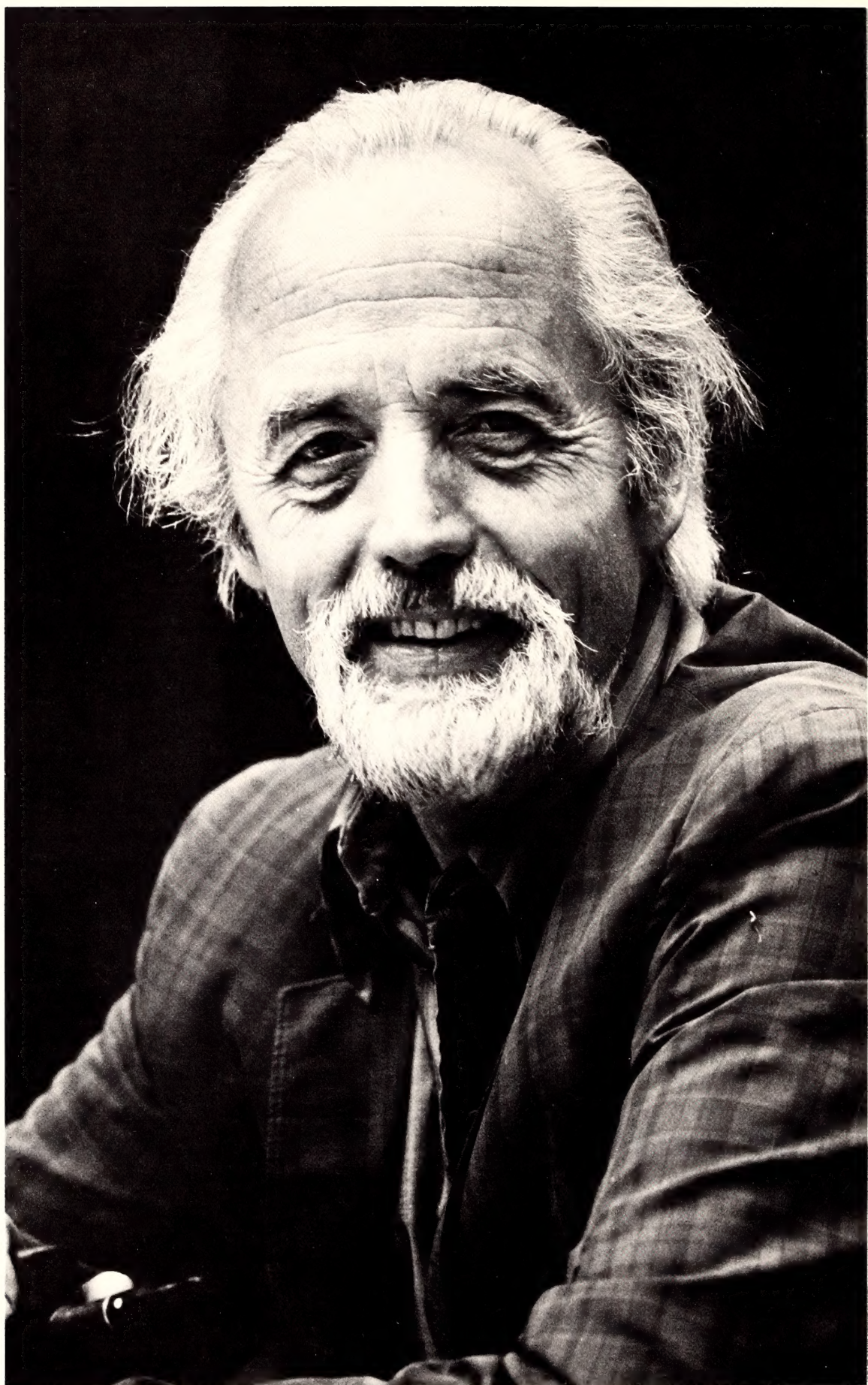
- 1989—FRANK VASEK, University of California, Riverside  
BARBARA ERTTER, University of California, Berkeley
- 1990—STEVEN TIMBROOK, Ganna Walska Lotusland Foundation, Montecito, CA  
THOMAS R. VAN DEVENDER, Arizona-Sonora Desert Museum, Tucson
- 1991—JAMES HENRICKSON, California State University, Los Angeles  
WAYNE R. FERREN, University of California, Santa Barbara
- 1992—BRUCE A. STEIN, The Nature Conservancy, Washington, D.C.  
WILLIAM L. HALVORSON, Channel Islands National Park, Ventura, CA
- 1993—JON E. KEELEY, Occidental College, Los Angeles, CA  
RHONDA L. RIGGINS, California Polytechnic State University, San Luis Obispo, CA

*Editor*—DAVID J. KEIL  
Biological Sciences Department  
California Polytechnic State University  
San Luis Obispo, CA 93407

Published quarterly by the  
California Botanical Society, Inc.  
Life Sciences Building, University of California, Berkeley 94720

Printed by Allen Press, Inc., Lawrence, KS 66044







Dedicated to botanical pursuits, Art Kruckeberg has distinguished himself as an eminent student of edaphic ecology. His work on serpentine endemism is classic. Known throughout western North America as an intrepid field researcher, Art's expertise spans ecology, population biology, systematics, phytogeography, evolution, conservation biology, and horticulture. Long before it became fashionable to be interdisciplinary, he was building bridges between these different fields of study. As a respected teacher and mentor, he has challenged and stimulated many students and colleagues. Born and educated in California, he has spent all 40 years of his professional career at the University of Washington. It is a pleasure to pay tribute to his outstanding botanical contributions.—MELINDA F. DENTON, Department of Botany, University of Washington, Seattle, WA 98195. Photo provided by Douglass M. Henderson, Department of Biological Sciences, University of Idaho, Moscow, ID 83843.



## TABLE OF CONTENTS

|  |     |
|--|-----|
| ALVERSON, EDWARD R., <i>Isopyrum stipitatum</i> (Ranunculaceae) in the Willamette Valley, Oregon .....   | 217 |
| ARGUS, GEORGE W., <i>Salix scouleriana</i> (Salicaceae) in Sonora, Mexico .....  | 135 |
| ARMSTRONG, WAYNE P., Noteworthy collections of <i>Wolffia</i> .....  | 283 |
| BARTOLOME, JAMES W. (see McCLARAN, MITCHEL P.)   |     |
| BAYER, RANDALL J., A systematic and phytogeographic study of <i>Antennaria aromatica</i> and <i>A. densifolia</i> (Asteraceae: Inuleae) in the western North American cordillera ..... | 248 |
| BECKING, RUDOLF W., Segregation of <i>Hastingsia serpentinicola</i> , sp. nov. from <i>Hastingsia alba</i> (Liliaceae: Aspholdeleae) .....   | 208 |
| BOWCUTT, FREDERICA S., Reappraisal of the range of <i>Phacelia vallicola</i> (Hydrophyllaceae) .....   | 51  |
| BREEDLOVE, DENNIS E., and JOSÉ LUIS LEÓN DE LA LUZ, A new species of <i>Daphnopsis</i> (Thymelaeaceae) from Baja California Sur, Mexico .....  | 266 |
| BROICH, S. L., Chromosome numbers of North American <i>Lathyrus</i> (Fabaceae) .....   | 41  |
| BUTTERWICK, MARY, Noteworthy collections of <i>Ephedra funerea</i> and <i>Melica imperfecta</i> .....  | 136 |
| CARTER, ANNETTA, Review of <i>Baja California Plant Field Guide</i> by Norman C. Roberts .....   | 287 |
| CHADWICK, ANN, and DAVID J. KEIL, Noteworthy collection of <i>Prunus fasciculata</i> var. <i>fasciculata</i> .....   | 32  |
| CHAMBERS, KENTON L., The taxonomic relationships of <i>Allocarya corallcarpa</i> (Boraginaceae) .....  | 280 |
| CHAMBERS, KENTON, and JACQUELINE GREENLEAF, <i>Gentiana setigera</i> is the correct name for <i>G. bisetata</i> (Gentianaceae) .....   | 49  |
| CLARK, CURTIS (see HARRINGTON, DANIEL F.)  |     |
| CESKA, ADOLF (see SAVALE, W. F., Jr.)  |     |
| DENISON, STELLA S., and DALE W. MCNEAL, A re-evaluation of the <i>Allium sanbornii</i> (Alliaceae) complex .....   | 122 |
| DEVINE, TIMOTHY B. (see Wagner, Warren H., Jr.)  |     |
| DOLAN, REBECCA W., and LAWRENCE F. LAPRÉ, Taxonomy of <i>Streptanthus</i> sect. <i>Biennes</i> , the <i>Streptanthus morrisonii</i> complex .....                                      | 33  |
| DOMÍNGUEZ-CADENA, RAYMUNDO (see LEÓN DE LA LUZ, JOSÉ LUIS)   |     |
| DORN, ROBERT D., Typification of <i>Salix geyeriana</i> (Salicaceae) .....   | 135 |
| ERTTER, BARBARA (see SHEVOCK, JAMES R.)  |     |
| FELGER, RICHARD S. (see REEDER, JOHN R.)   |     |
| GOTTLIEB, L. D., Floral pigmentation patterns in <i>Clarkia</i> (Onagraceae) .....   | 1   |
| GREENLEAF, JACQUELINE (see CHAMBERS, KENTON)   |     |
| HALVORSON, WILLIAM L., Review of <i>North American Terrestrial Vegetation</i> edited by Michael G. Barbour and W. Dwight Billings .....  | 219 |
| HAMMER, SAMUEL, Phytogeographical notes on acidophilous <i>Cladonia</i> species in California .....  | 169 |
| HARRINGTON, DANIEL F., and CURTIS CLARK, Reduction in light reflectance of leaves of <i>Encelia densifolia</i> (Asteraceae) by trichome wetting 180                                    |     |
| HICKMAN, JAMES C., Points of View: Response to Reveal .....  | 218 |
| HILSENBECK, RICHARD A., A new species of <i>Siphonoglossa</i> (Acanthaceae) and some infrageneric transfers .....  | 198 |
| HILSENBECK, RICHARD A. (see RALSTON, BARBARA E.)   |     |
| HORN, SALLY P., Postfire vegetation development in the Costa Rican paramos .....   | 93  |
| JOKERST, JAMES D. (see Shevock, James R.)  |     |



|   |     |
|---|-----|
| JOYAL, ELAINE, Noteworthy collections of <i>Astragalus curvicaupus</i> var. <i>subglaber</i> , <i>Collomia debilis</i> var. <i>larsenii</i> , and <i>Rudbeckia occidentalis</i> var. <i>montana</i> from Oregon ..... | 53  |
| JOYAL, ELAINE, <i>Myosotis latifolia</i> and not <i>M. sylvatica</i> (Boraginaceae) in California .....   | 131 |
| KEELEY, JON E., Review of <i>The Biogeography of Fire in the San Bernardino Mountains of California—A Historical Study</i> by Richard A. Minnich .....  | 287 |
| KELLEY, WALTER A., Comments and notes on <i>Portulaca</i> in California .....   | 281 |
| KELLEY, WALTER A., and DIETER H. WILKEN, Several noteworthy collections from Colorado .....   | 285 |
| KEIL, DAVID J., Review of <i>A Guide to Wildlife Habitats of California</i> by K. E. Mayer and W. F. Laudenslayer .....   | 57  |
| KEIL, DAVID J. (see CHADWICK, ANN)  |     |
| KNIGHT, PAUL (see SPELLENBERG, RICHARD)   |     |
| KRUCKEBERG, A. R., Review of <i>Soil-Plant Relations: An Ecological Approach</i> by D. W. Jeffrey .....   | 219 |
| KUIJT, JOB, A note on the germination and establishment of <i>Phoradendron californicum</i> (Viscaceae) .....   | 175 |
| LANDRUM, LESLIE R., The generic position of <i>Myrtus alternifolia</i> and notes on <i>Calycolpus</i> (Myrtaceae) .....   | 9   |
| LAPRÉ, LAWRENCE F. (see DOLAN, REBECCA W.)  |     |
| LEÓN DE LA LUZ, JOSÉ LUIS (see BREEDLOVE, DENNIS E.)  |     |
| LEÓN DE LA LUZ, JOSÉ LUIS, and RAYMUNDO DOMÍNGUEZ-CADENA, Flora of the Sierra de la Laguna, Baja California Sur, Mexico .....   | 61  |
| LUCKOW, MELISSA, Review of <i>Trees and Shrubs of Trans-Pecos Texas</i> by A. Michael Powell .....  | 56  |
| MASON, CHARLES T., Infraspecific name changes in <i>Limnanthes</i> (Limnanthaceae) .....  | 50  |
| MCCLARAN, MITCHEL P., and JAMES W. BARTOLOME, Effect of <i>Quercus douglasii</i> (Fagaceae) on herbaceous understory along a rainfall gradient .....  | 141 |
| MCLEOD, MALCOLM G., Review of <i>Inventory of Rare and Endangered Vascular Plants of California</i> edited by James P. Smith and Ken Berg .....   | 54  |
| MCNEAL, DALE W. (see DENISON, STELLA S.)  |     |
| NESOM, GUY L., <i>Macromeria alba</i> (Boraginaceae), a new species from Tamaulipas, Mexico .....   | 28  |
| PARSONS, DAVID J., and THOMAS J. STOHLGREN, Effects of varying fire regimes on annual grasslands in the southern Sierra Nevada of California .....  | 154 |
| PASSINI, MARIE-FRANOISE, and NICOLE PINEL, Ecology and distribution of <i>Pinus lagunae</i> in the Sierra de la Laguna, Baja California Sur, Mexico .....   | 84  |
| PATTERSON, ROBERT, Taxonomic relationships of <i>Gilia maculata</i> (Polemoniaceae) .....   | 15  |
| PETERSON, PAUL M., A re-evaluation of <i>Bealia mexicana</i> (Poaceae: Eragrostideae) .....   | 260 |
| PHILLIPS, H. WAYNE, Noteworthy collection of <i>Goodyera repens</i> .....   | 174 |
| PINEL, NICOLE (see PASSINI, MARIE-FRANÇOISE)  |     |
| PINKAVA, DONALD J., Review of <i>Colorado Flora: Western Slope</i> by William A. Weber .....  | 56  |
| RALSTON, BARBARA E., and RICHARD A. HILSENBECK, Taxonomy of the <i>Opuntia schottii</i> complex (Cactaceae) in Texas .....  | 221 |
| REEDER, JOHN R., and RICHARD S. FELGER, The <i>Aristida californica</i> - <i>glabrata</i> complex (Gramineae) .....   | 187 |
| REVEAL, JAMES L., Points of View: On the modern death of David Douglas ..   | 137 |
| SAVALE, W. F., Jr., and ADOLF CESKA, Noteworthy collections of <i>Wolffia columbiana</i> .....  | 153 |
| SCHIERENBECK, KRISTINA A., Noteworthy collection of <i>Polygonum marinense</i> .....  | 207 |



|   |     |
|---|-----|
| SCHMIDT, CLIFFORD L., Review of <i>Guide to the Regional Parks Botanic Garden</i><br>by Walter Knight and Irja Knight .....   | 54  |
| SHELLY, J. STEPHEN, Biosystematic studies of <i>Phacelia capitata</i> (Hydrophyl-<br>laceae), a species endemic to serpentine soils in southwestern Oregon .....                            | 232 |
| SHEVOCK, JAMES R., BARBARA ERTTER, and JAMES D. JOKERST, <i>Monardella</i><br><i>beneolens</i> (Lamiaceae), a new species from the crest of the southern Sierra<br>Nevada, California ..... | 271 |
| SPELLENBERG, RICHARD, and PAUL KNIGHT, A new species of <i>Erigeron</i> (Aster-<br>eaceae: Astereae) from central New Mexico .....  | 115 |
| STOHLGREN, THOMAS J. (see PARSONS, DAVID J.)  |     |
| VINCENT, KARL A., Noteworthy collection of <i>Penstemon venustus</i> (Scrophu-<br>lariaceae) from California .....  | 53  |
| WAGNER, WARREN H., JR., and TIMOTHY B. DEVINE, Moonworts ( <i>Botrychium</i> :<br>Ophioglossaceae) in the Jonesville area, Butte and Tehama Counties, Cal-<br>ifornia .....                 | 131 |
| WILKEN, DIETER H. (see KELLEY, WALTER A., and DIETER H. WILKEN)   |     |
| WILSON, PAUL, Noteworthy collection of <i>Pallavicinia lyellii</i> (Hepaticae: Pal-<br>laviciaceae) from California .....   | 53  |
| ZIKA, PETER F., Noteworthy collection of <i>Panicum rigidulum</i> .....   | 207 |



33  
f.

## MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

## Contents

|   |            |
|---|------------|
| FLORAL PIGMENTATION PATTERNS IN <i>CLARKIA</i> (ONAGRACEAE)<br><i>L. D. Gottlieb</i>  | 1          |
| THE GENERIC POSITION OF <i>MYRTUS ALTERNIFOLIA</i> AND NOTES ON <i>CALYCOLPUS</i> (MYRTACEAE)<br><i>Leslie R. Landrum</i>   | 9          |
| TAXONOMIC RELATIONSHIPS OF <i>GILIA MACULATA</i> (POLEMONIACEAE)<br><i>Robert Patterson</i>   | 15         |
| <i>MACRONEMA ALBA</i> (BORAGINACEAE), A NEW SPECIES FROM TAMAULIPAS, MEXICO<br><i>Guy L. Nesom</i>  | 28         |
| TAXONOMY OF <i>STREPTANTHUS</i> SECT. <i>BIENNES</i> , THE <i>STREPTANTHUS MORRISONII</i> COMPLEX (BRASSICACEAE)<br><i>Rebecca W. Dolan and Lawrence F. LaPre</i> | 33         |
| CHROMOSOME NUMBERS OF NORTH AMERICAN <i>LATHYRUS</i> (FABACEAE)<br><i>Steven L. Broich</i>  | 41         |
| NOTES   |            |
| <i>GENTIANA SETIGERA</i> IS THE CORRECT NAME FOR <i>G. BISETAEA</i> (GENTIANACEAE)<br><i>Kenton L. Chambers and Jacqueline Greenleaf</i>                          | 49         |
| INFRASPECIFIC NAME CHANGES IN <i>LIMNANTHES</i> (LIMNANTHACEAE)<br><i>Charles T. Mason</i>  | 50         |
| REAPPRAISAL OF THE RANGE OF <i>PHACELIA VALLICOLA</i> (HYDROPHYLLACEAE)<br><i>Frederica Bowcutt</i>   | 51         |
| NOTEWORTHY COLLECTIONS  |            |
| CALIFORNIA  | 32, 53     |
| OREGON  | 53         |
| REVIEWS   | 54         |
| ANNOUNCEMENTS   | 27, 40, 60 |





MADROÑO (ISSN 0024-9637) is published quarterly by the California Botanical Society, Inc., and is issued from the office of the Society, Herbarium, Life Sciences Building, University of California, Berkeley, CA 94720. Subscription rate: \$30 per calendar year. Subscription information on inside back cover. Established 1916. Second-class postage paid at Berkeley, CA, and additional mailing offices. Return requested. POSTMASTER: Send address changes to James R. Shevock, Botany Dept., California Academy of Sciences, San Francisco, CA 94118.

*Editor*—DAVID J. KEIL

Biological Sciences Department  
California Polytechnic State University  
San Luis Obispo, CA 93407

*Board of Editors*

Class of:

- 1989—FRANK VASEK, University of California, Riverside, CA  
BARBARA ERTTER, University of California, Berkeley, CA  
1990—STEVEN TIMBROOK, Ganna Walska Lotusland Foundation, Montecito, CA  
THOMAS R. VAN DEVENDER, Arizona-Sonora Desert Museum, Tucson, AZ  
1991—JAMES HENRICKSON, California State University, Los Angeles, CA  
WAYNE R. FERREN, JR., University of California, Santa Barbara, CA  
1992—BRUCE A. STEIN, The Nature Conservancy, Washington, D.C.  
WILLIAM L. HALVORSON, Channel Islands National Park, Ventura, CA  
1993—JON E. KEELEY, Occidental College, Los Angeles, CA  
RHONDA L. RIGGINS, California Polytechnic State University, San Luis Obispo, CA

---

CALIFORNIA BOTANICAL SOCIETY, INC.

OFFICERS FOR 1988–89

- President:* JOHN L. STROTHER, University Herbarium, University of California, Berkeley, CA 94720  
*First Vice President:* JAMES AFFOLTER, Botanical Garden, University of California, Berkeley, CA 94720  
*Second Vice President:* JAMES HENRICKSON, California State University, Los Angeles, CA 90032  
*Recording Secretary:* RODNEY G. MYATT, Department of Biological Sciences, San Jose State University, San Jose, CA 95192  
*Corresponding Secretary:* JAMES R. SHEVOCK, Department of Botany, California Academy of Sciences, San Francisco, CA 94118  
*Treasurer:* THOMAS F. DANIEL, Department of Botany, California Academy of Sciences, San Francisco, CA 94118  
*Financial Officer:* CHERIE L. WETZEL, Department of Biology, City College of San Francisco, 50 Phelan Ave., San Francisco, CA 94112

The Council of the California Botanical Society consists of the officers listed above plus the immediate *Past President*, DALE MCNEAL, Department of Biological Sciences, University of the Pacific, Stockton, CA 95211; the *Editor* of MADROÑO; three elected *Council Members*: JOHN MOORING, Department of Biology, University of Santa Clara, Santa Clara, CA 95053; BARBARA ERTTER, Herbarium, Botany Department, University of California, Berkeley, CA 94720; ELIZABETH MCCLINTOCK, Herbarium, Botany Department, University of California, Berkeley, CA 94720; and a *Graduate Student Representative*, VALERIE HALEY, Department of Biological Sciences, San Jose State University, San Jose, CA 95192.

|   |
|---|
| THIS PUBLICATION IS PRINTED ON ACID-FREE PAPER. |
|---|



# FLORAL PIGMENTATION PATTERNS IN *CLARKIA* (ONAGRACEAE)

L. D. GOTTLIEB

Department of Genetics, University of California,  
Davis, CA 95616

## ABSTRACT

The pattern of anthocyanin pigmentation on flower petals of species of *Clarkia* sections *Rhodanthos* and *Godetia* is reviewed. The petals have large spots, blotches, or bands of red-purple color near the base, the center, the upper margin or in several positions, or are unspotted. A recent genetic analysis in *C. gracilis* revealed that the large central petal spot characteristic of subsp. *sonomensis* is allelic to a basal petal spot in subsp. *gracilis* that is normally not expressed because of the action of a modifier gene. Since *Clarkia* species display only a small number of discrete pigmentation patterns, I suggest that the major components of pattern differences among them are not complex from a genetic standpoint. Novel patterns can be assembled by substituting alleles at relatively few loci. Additional genes presumably contribute to various details of the patterns.

In many genera of plants, the flower displays more differences from species to species than any other plant part, varying, for example, in size, shape, outline, texture, orientation, and color as well as in features of scent, nectar, and pollen. Many floral traits serve to attract and reward specific pollinators. Although the flower has obvious and important adaptive significance, the genetic basis of floral differences between species has been worked out in only a few cases (Gottlieb 1984). Genetic studies might reveal whether new floral phenotypes result from the activities of a relatively small number of (major) genes or originate only after the accumulation of numerous genetic differences. In addition, when the same or similar phenotype appears in a number of species, it is important to determine whether this reflects the activities of the same subset of genes or convergence based on the independent appearance of new combinations of genes. Information on these issues will help us to understand how morphological differences evolve in plants.

Floral differentiation involving changes in both structural morphology and pigmentation patterns is particularly important among species of *Clarkia* (Onagraceae) native to California. Overall floral differentiation in *Clarkia* is closely associated with the pollination system (MacSwain et al. 1973). Indeed, much of the adaptive radiation in the genus has primarily involved the flower, so that if plants of different species were stripped of their flowers, they would be nearly identical in appearance (MacSwain et al. 1973). The genus has long been used as a model system for studies of plant evolu-



tionary biology, beginning with the elegant biosystematic and cytogenetic studies of Professor Harlan Lewis and his students and colleagues (Lewis 1953, 1962, 1973; Lewis and Lewis 1955). More recent studies of *Clarkia* include examination of genetic differentiation among species using data from electrophoretic analysis of isozymes (Gottlieb and Weeden 1979; Pichersky and Gottlieb 1983; Odrzykoski and Gottlieb 1984; Soltis et al. 1987), and reconstructions of species relationships using restriction endonuclease analysis of chloroplast DNA (Sytsma and Gottlieb 1986a, b).

The most common floral type in diploid *Clarkia* species is the "godetia" flower which characterizes sections *Godetia*, *Rhodanthos*, *Peripetasma*, and *Fibula*, totalling about two dozen species. The godetia flower is held upright and is shaped like a bowl. The four petals are obovate to fan-shaped and are not much narrowed at the base. Although their structure, size, and shape are generally similar, the pattern of anthocyanin pigmentation, particularly on the petals, varies strikingly. The petals may have large spots, blotches, or bands of reddish-purple color near the base, the center, the upper margin, or sometimes in several of these positions. Alternatively, the petals may have hundreds of very small (2–8 cells) red or purple flecks, particularly near the center, or be unspotted. The characteristic lavender to reddish-purple pigments have been identified as glycoside derivatives of malvidin, supplemented with derivatives of cyanidin and delphinidin (Soltis 1986). The large spots or flecks appear to result from locally elevated levels of the same pigments, though in different proportion than in the petal background (Dorn and Bloom 1984). Although the petals are generally pigmented throughout, those of many species also have large white areas of no pigmentation. Anthocyanins may also be present or absent on filaments and anthers, the stigma, and the floral tube.

#### PETAL PATTERN IN *CLARKIA GRACILIS*

The petal pigmentation patterns of species assigned to *Godetia* and *Rhodanthos* can be divided into four major types: central spot only, distal spot only, basal band only, and unspotted. In addition, the petals of several species have more than one large pigmented spot. Since nearly all *Clarkia* species are strongly reproductively isolated, the genetic basis of the petal patterns cannot be directly studied. However, it has been possible to carry out a genetic study between two subspecies of *Clarkia gracilis*, an allotetraploid species in *Rhodanthos*, derived from the diploid *C. amoena* subsp. *huntiana* and an extinct species related to *C. lassenensis* and *C. arcuata* (Abdel-Hameed and Snow 1972).

*Clarkia gracilis* includes four interfertile subspecies that, as a group, display three of the four basic petal patterns described above. Sub-



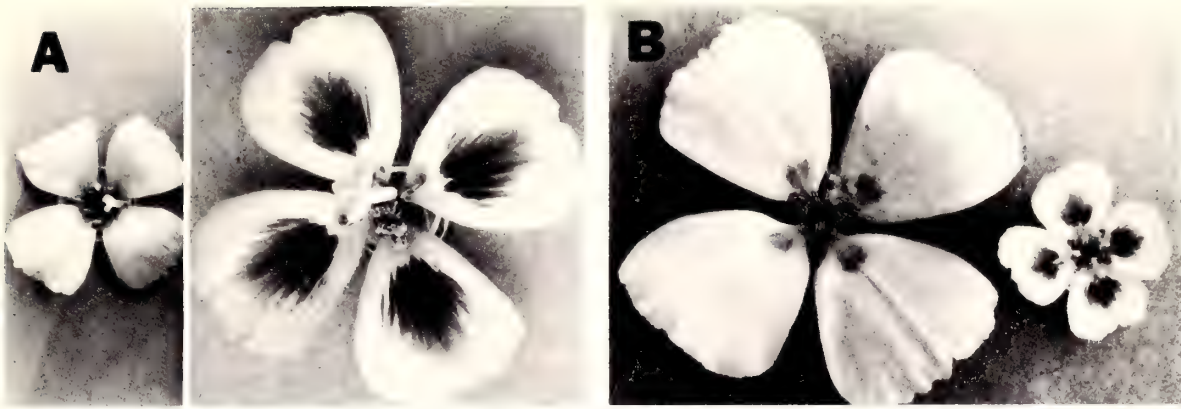


FIG. 1. (A) Flowers of *C. gracilis* subsp. *gracilis* (left), and *C. gracilis* subsp. *sonomensis* (right); (B) Flowers of  $F_2$  recombinant with large flower and basal spot, and an  $F_2$  recombinant with small flower and central spot.

species *sonomensis* has large pink petals each with a large central red-purple spot, subsp. *albicaulis* and *tracyi* have large pink petals each with an intense red-purple band of color across the base, and subsp. *gracilis* has small unspotted pink petals. The three subspecies with large petals have a marked protandry (the pollen is released 3–5 days before the stigma becomes receptive) and are outcrossing. Subspecies *gracilis* is predominantly self-pollinating because when its flowers open, the stigma is already receptive and at the same height as the adjacent anthers. The four subspecies have a high genetic identity (Holsinger and Gottlieb 1988) and a moderate amount of chromosomal structure divergence (Abdel-Hameed and Snow 1968, 1972).

The petals of subsp. *sonomensis* are about 2.5 times longer and 4 times wider than those of subsp. *gracilis*. Numerous genes probably contribute to the size difference because the petal sizes of both parents were not recovered in a large  $F_2$  (238 plants) or backcross progenies from hybrids between them (Gottlieb and Ford 1988). Although petal size behaves like a classical quantitative trait, the presence/absence of petal spots is controlled by a single gene. Thus a recent genetic analysis (Gottlieb and Ford 1988) revealed that subsp. *gracilis* has a gene governing basal petal spot that is not normally expressed (Fig. 1). The gene is allelic to one for central spot in subsp. *sonomensis*, but is not expressed because it is inhibited by a gene at another locus (Gottlieb and Ford 1988). Allelism of central petal spot, basal “band” (see below), as well as unspotted petal had previously been reported in the related diploid *C. rubicunda* (Rasmuson 1921; Hiorth 1940). Additional genes modify the size and exact position of the central spot. For example, the width of the central spot can vary from very narrow, with only a few dozen files of pigmented cells, to a broad blotch of color about half or more the width of the petal. The genetics of these modifications have not yet been analyzed.



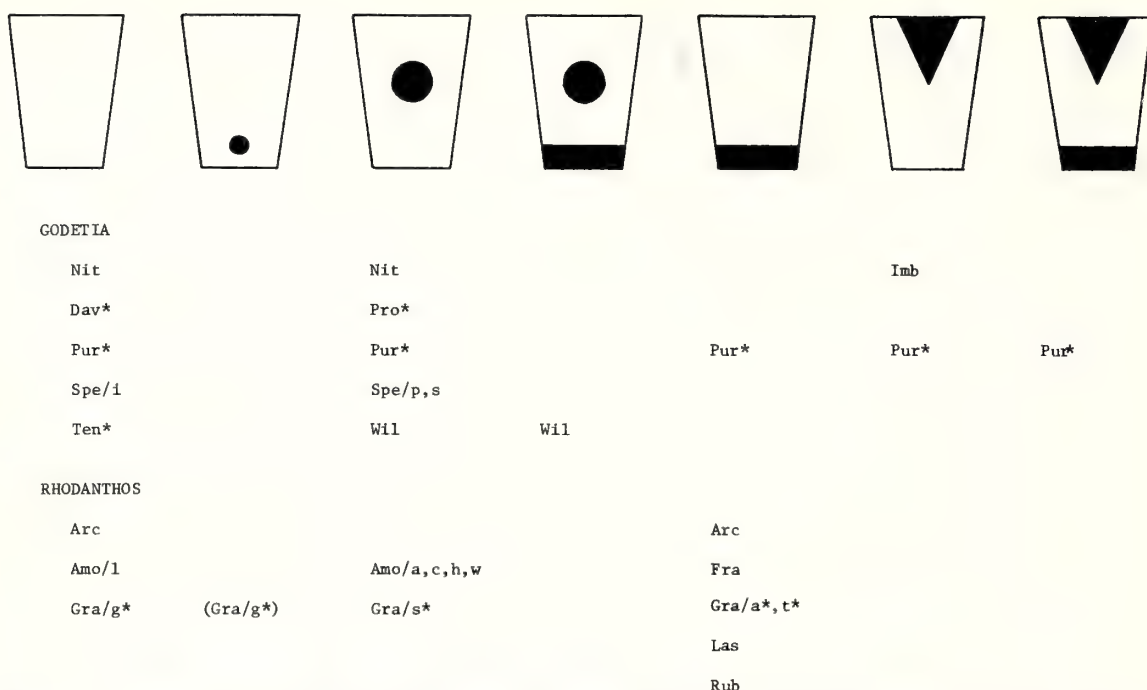


FIG. 2. Diagram of petal pigmentation patterns in species of *Clarkia* sections *Godetia* and *Rhodanthos*. An asterisk indicates the species is polyploid. Names of the taxa are abbreviated as follows: *C. arcuata* (ARC); *C. amoena* subsp. *amoena* (AMO/a), subsp. *caurina* (AMO/c), subsp. *huntiana* (AMO/h), subsp. *lindleyi* (AMO/l), subsp. *whitneyi* (AMO/w); *C. davyi* (DAV); *C. franciscana* (FRA); *C. gracilis* subsp. *albicaulis* (GRA/a), subsp. *gracilis* (GRA/g), subsp. *sonomensis* (GRA/s), subsp. *tracyi* (GRA/t); *C. imbricata* (IMB); *C. lassenensis* (LAS); *C. nitens* (NIT); *C. prostrata* (PRO); *C. purpurea* (PUR); *C. rubicunda* (RUB); *C. speciosa* subsp. *immaculata* (SPE/i), subsp. *polyantha* (SPE/p), subsp. *speciosa* (SPE/s); *C. tenella* (TEN); *C. williamsonii* (WIL).

### PETAL PATTERN IN RELATED *CLARKIA* SPECIES

Knowledge of the genetic basis of petal pigmentation in *C. gracilis* suggests that many of the petal patterns that distinguish other species in *Godetia* and *Rhodanthos* may also be governed by single genes. The petal patterns of all the species in the two sections are diagrammed in Figure 2. Most species are spotless, or have a central spot or a basal band of color. Two species have a wedge-shaped spot that extends from the center of the petal to its upper margin. Four species (*C. arcuata*, *C. nitens*, *C. purpurea*, and *C. williamsonii*) are polymorphic for petal pattern. Of them, the most polymorphic is *C. purpurea*, an allohexaploid that has at least five common patterns, all frequently observed in the same population.

The many variants of *C. purpurea* probably reflect its hexaploidy and the consequences of occasional hybridization followed by sorting out of new homozygous genotypes by virtue of its self-pollinating breeding system. Lewis and Lewis (1955, p. 304) reported a cross between the small-flowered *C. purpurea* subsp. *quadrivulnera* and the large-flowered subsp. *viminea* that showed continuous segregation for petal size in an  $F_2$  but sharp segregation for petal color and pattern, similar to results obtained in *C. gracilis* (Gottlieb and Ford



1988). Apparently homologous genes affecting floral pigmentation in diploid and tetraploid derivatives have been described in *Primula* (De Winton and Haldane 1933) and *Gossypium* (Harland 1935).

*Clarkia williamsonii* often exhibits both central spot and basal band on its petals. Since the two are known to be allelic in another *Clarkia* (Rasmuson 1921; Hiorth 1940), their combined presence in a true-breeding pattern in a diploid species is consistent with duplication of the coding genes, analogous to duplication of genes encoding isozymes described for a number of diploid *Clarkia* species (Gottlieb 1977; Pichersky and Gottlieb 1983). Alternatively, the multiple spots may reflect activation of a single gene at different times during petal development.

Since clarkias display only a small number of discrete petal patterns, and since differences in several of them are allelic, it is plausible that the presence of the same petal pattern reflects utilization of the same subset of genes, and that different patterns result from simple allelic substitutions. Many additional genes presumably contribute to the details of floral pigmentation, for example, the particular pigment mix, the size and shape of the spots (round versus wedge-shaped) and their exact position on the petal. The inheritance of the major components of floral pattern, for example, spot presence/absence and spot position, however, need not be regarded as complex. New patterns can be assembled by substituting alleles at a small number of loci, not unlike the situation described for cuticular patterns of chaetae and trichomes in *Drosophila* (Garcia-Bellido 1983).

#### THE BASAL SPOT GENE IN SUBSP. *GRACILIS*

The recovery of an allele for basal spot from the unspotted subsp. *gracilis* poses interesting questions about its origin. The basal band of color in the related subspecies, *albicaulis* and *tracyi*, extends completely across the petal base whereas the subsp. *gracilis* spot is small, more or less round, and does not extend to the edges of the petal. The gene for large central spot in subsp. *sonomensis* most likely comes from *C. amoena* subsp. *huntiana* which also has a similar central petal spot, and the gene for basal band characteristic of subsp. *albicaulis* and *tracyi* probably derives from a species related to the diploids *C. lassenensis* and *C. arcuata* which have a basal petal band. The two other diploid species in *Rhodanthos* also have a basal petal band.

Natural hybridization between subsp. *gracilis* and subsp. *sonomensis* has been documented (Lewis and Lewis 1955, p. 280), and it is interesting that plants with small petals and central spots that otherwise resemble subsp. *gracilis* were identified. Were some plants to show the novel basal spot, an observer would not know that its



coding gene already existed, and was simply “released” from inhibition. Many loci may include alleles that normally remain unexpressed, and segregation following hybridization, which is frequent in plants, may place such alleles as well as normally expressed alleles under new patterns of regulation resulting in the abrupt appearance of new forms. Though they might seem like macromutations, the novel phenotypes could be simply explained. Novel phenotypes would also occur when a rare recessive allele that governs a morphological trait in an outcrosser becomes homozygous and is expressed following hybridization with a related selfer (Rick and Smith 1953).

The progenies between subsp. *gracilis* and subsp. *sonomensis* also segregated for several other differences in their pigmentation patterns (Gottlieb and Ford 1988). The background petal color of subsp. *sonomensis* is frequently uniform. However, in some individuals, the basal quarter of each petal lacks anthocyanin pigments and is bright white, giving the appearance of a “white cup,” especially when the flower is newly opened. Presence versus absence of white cup proved to be governed by a single locus, with white cup (representing absence of pigment) recessive. A single gene was also identified that governs presence versus absence of dark red pigmentation on the inner surface of the floral tube, and another gene was found that controls presence versus absence of color on the anthers and filaments. In all, five genes that affect pattern of anthocyanin color on the petals and other floral organs were identified in addition to the polygenic control of petal size. The white cup pattern is present in many *Clarkia* species including *C. arcuata*, *C. bottae*, *C. davyi*, and *C. imbricata* as well as in *C. gracilis* subspp. *albicaulis* and *tracyi*, and its genetic basis may be similar to that found in subsp. *sonomensis*. Presence or absence of color on the floral tube also distinguishes *Clarkia* species.

### CONCLUSIONS

It is not known whether the differences in pigmentation pattern of *Clarkia* species were selected by different pollinators. MacSwain et al. (1973) believed that the differences in petal spotting may play a role in determining pollinator constancy on individual trips from the nest, thus serving to increase the frequency of intraspecific pollinations. Some of the novel variants of *C. gracilis* constructed during the genetic study may be useful to test hypotheses concerning floral pattern and pollination system. Appropriate variations can be introduced into different habitats and monitored to observe pollinator preferences. In such studies, it would be possible to focus on individual traits such as spot position or white cup or on different trait combinations.



The discovery that subsp. *gracilis* has a gene for basal petal spot that is not normally expressed because of the action of a second gene emphasizes the importance of genetic studies for understanding morphological differences between species. This may be particularly significant in plants where interspecific hybridization and allopolyploidy are prevalent. Many novel phenotypes in plants may result from new modes of gene regulation brought about by the juxtaposition of divergent genetic materials rather than by accumulation of novel genes.

The pigmentation pattern on petals and other floral organs commonly varies among species in many plant genera. Important genetic studies in cultivated plants include the analysis of Japanese morning glories which revealed a large number of single genes that confer sharply distinct pigment patterns on the petals such as *blizzard*, *flecked*, *lined*, *striated*, *speckled*, and *smearly* (Imai 1931). Other genetic studies were carried out in *Primula sinensis* (De Winton and Haldane 1933). Few studies have been done in wild plants although many reports are available of pattern differences between and within species. A recently published example is *Platystemon californicus*, which exhibits at least six color patterns on its showy flowers that appear to be roughly correlated with geographical distribution (Hannan 1981). A number of species with flower color polymorphism are listed in Hannan (1981) and Kay (1978).

The flower is a complex structure in which many specialized tissues and cell types form distinctive organs in a precise and orderly manner. The differentiation of structures is most likely independent of pigmentation pattern, and this is one reason the patterns may be changed by few genes. Although the patterns may have a simple and readily modified developmental basis, pigment patterns are likely to have complex effects on pollination and eventual seed set. Changed patterns appear to be particularly important in annual plants like *Clarkia* in which most species are outcrossing, and often as many as five or six species grow intermixed beneath the oak trees on the same Sierran hillside.

#### LITERATURE CITED

- ABDEL-HAMEED, F. and R. SNOW. 1968. Cytogenetic studies in *Clarkia*, sect. *primigenia*. IV. A cytological survey of *Clarkia gracilis*. Amer. J. Bot. 55:1047–1054.
- and ———. 1972. The origin of the allotetraploid *Clarkia gracilis*. Evolution 26:74–93.
- DE WINTON, D. and J. B. S. HALDANE. 1933. The genetics of *Primula sinensis*. II. Segregation and interaction of factors in the diploid. J. Genetics 27:1–44.
- DORN, P. S. and W. L. BLOOM. 1984. Anthocyanin variation in an introgressive complex in *Clarkia*. Biochem. Syst. Ecol. 12:311–314.
- GARCIA-BELLIDO, A. 1983. Comparative anatomy of cuticular patterns in the genus *Drosophila*. Pp. 227–259 in B. C. Goodwin, N. Holder, and C. C. Wylie (eds.), Development and evolution. Cambridge Univ. Press, Cambridge.



- GOTTLIEB, L. D. 1977. Evidence for duplication and divergence of the structural gene for phosphoglucose isomerase in diploid species of *Clarkia*. *Genetics* 86: 289–307.
- . 1984. Genetics and morphological evolution in plants. *Amer. Naturalist* 123:681–709.
- and V. S. FORD. 1988. Genetic studies of the pattern of floral pigmentation in *Clarkia gracilis*. *Heredity* 60:237–246.
- and N. F. WEEDEN. 1979. Gene duplication and phylogeny in *Clarkia*. *Evolution* 33:1024–1039.
- HANNAN, G. L. 1981. Flower color polymorphism and pollination biology of *Platystemon californicus* Benth. (Papaveraceae). *Amer. J. Bot.* 68:233–243.
- HARLAND, S. C. 1935. Homologous genes for anthocyanin pigmentation in new and old world cottons. *J. Genetics* 30:465–476.
- HIORTH, G. 1940. Eine Serie multipler Allele für Blütenzeichnungen bei *Godetia amoena*. *Hereditas* 26:441–453.
- HOLSINGER, K. and L. D. GOTTLIEB. 1988. Isozyme variability in the tetraploid *Clarkia gracilis* (Onagraceae) and its diploid relatives. *Syst. Bot.* 13:1–6.
- IMAI, Y. 1931. Analysis of flower color in *Pharbitis nil*. *J. Genetics* 24:203–224.
- KAY, Q. O. N. 1978. The role of preferential and assortive pollination in the maintenance of flower color polymorphisms. Pp. 175–190 in A. J. Richards (ed.), *The pollination of flowers by insects*. Academic Press, London.
- LEWIS, H. 1953. The mechanism of evolution in the genus *Clarkia*. *Evolution* 7: 1–20.
- . 1962. Catastrophic selection as a factor in speciation. *Evolution* 16:257–271.
- . 1973. The origin of diploid neospecies in *Clarkia*. *Amer. Naturalist* 107: 161–170.
- and M. E. LEWIS. 1955. The genus *Clarkia*. *Univ. Calif. Publ. Bot.* 20:241–392.
- MACSWAIN, J. W., P. H. RAVEN, and R. W. THORP. 1973. Comparative behavior of bees and Onagraceae. IV. *Clarkia* bees of the western United States. *Univ. Calif. Publ. Entom.* 70:1–80.
- ODRZYKOSKI, I. J. and L. D. GOTTLIEB. 1984. Duplications of genes coding 6-phosphogluconate dehydrogenase in *Clarkia* (Onagraceae) and their phylogenetic implications. *Syst. Bot.* 9:479–489.
- PICHERSKY, E. and L. D. GOTTLIEB. 1983. Evidence for duplication of the structural genes coding plastid and cytosolic isozymes of triose phosphate isomerase in diploid species of *Clarkia*. *Genetics* 105:421–436.
- RASMUSON, H. 1921. Beiträge zu einer genetischen Analyse zweier *Godetia*-Arten und ihrer Bastarde. *Hereditas* 2:143–289.
- RICK, C. M. and P. G. SMITH. 1953. Novel variation in tomato species hybrids. *Amer. Naturalist* 87:359–373.
- SOLTIS, P. S. 1986. Anthocyanin variation in *Clarkia* (Onagraceae). *Biochem. Syst. and Ecol.* 14:487–489.
- , D. E. SOLTIS, and L. D. GOTTLIEB. 1987. Phosphoglucomutase gene duplications in *Clarkia* (Onagraceae) and their phylogenetic implications. *Evolution* 41:667–671.
- SYTSMA, K. J. and L. D. GOTTLIEB. 1986a. Chloroplast DNA evolution and phylogenetic relationships in *Clarkia* sect. *Peripetasma* (Onagraceae). *Evolution* 40: 1248–1261.
- and ———. 1986b. Chloroplast DNA evidence for the origin of the genus *Heterogaura* from a species of *Clarkia* (Onagraceae). *Proc. Nat. Acad. Sci. U.S.A.* 83:5554–5557.

(Received 27 Jul 1988; revision accepted 7 Oct 1988.)



# THE GENERIC POSITION OF *MYRTUS ALTERNIFOLIA* AND NOTES ON *CALYCOLPUS* (MYRTACEAE)

LESLIE R. LANDRUM

Department of Botany, Arizona State University,  
Tempe, AZ 85287

## ABSTRACT

*Myrtus alternifolia*, a species of long standing uncertain generic affinities, is transferred to *Calycolpus*. This transfer is based on characteristics of the seed coat, embryo, calyx, anthers, and vessel elements. A revised description of *Calycolpus* is provided.

## RESUMEN

*Myrtus alternifolia*, una especie que desde hace mucho tiempo ha sido de afinidades genéricas inciertas, se transfiere a *Calycolpus*. Este cambio se basa en características de la testa de la semilla, el embrión, el cáliz, las anteras, y los elementos vasculares. Se provee una descripción revisada de *Calycolpus*.

*Myrtus alternifolia* Gleason was described in 1939 and placed in *Myrtus* L. because Gleason believed it to be congeneric with species of *Myrtus* (*M. myricoides* Kunth, *M. stenophylla* Oliver ex Thurn, *M. roraimensis* N. E. Brown) now considered to belong to *Ugni* Turcz. McVaugh (1969) in his revision of the Myrtaceae of the Guayana Highland, recognized that *Myrtus alternifolia* was not a species of *Ugni* and that it probably did not belong to *Myrtus*, but lacking any clear evidence of its true affinities, did not transfer it to any genus.

*Myrtus*, the type genus of the Myrtaceae, was once very inclusive, accommodating perhaps a quarter of the family in the early nineteenth century. Since then a progressively smaller percentage of species has been assigned to *Myrtus*. I agree with McVaugh (1968) that *Myrtus* probably does not include any American species. Scott (1979) and Byrnes (1982) have expressed the opinion that certain Australasian species belong to *Myrtus*, but if those are excluded, the genus consists of only the Mediterranean *Myrtus communis* L. *Myrtus alternifolia* differs from *M. communis* in many morphological characters, most notably in embryo structure. The two species are also geographically widely separated. Thus, extraction of *Myrtus alternifolia* from *Myrtus* is warranted.

I am now monographing American genera of the Myrtinae with hard seed coats, the group to which *Myrtus alternifolia* belongs, and have considered the following genera to be possible acceptors for *M. alternifolia*: *Calycolpus* Berg, *Mosiera* Small, *Myrteola* O. Berg, *Psidium* L., and *Ugni*. Thanks to a collection of *M. alternifolia* with



mature seeds recently made by Bruce Holst of the Missouri Botanical Garden and a survey of seed coat characters in the Myrtinae undertaken at Arizona State University (Landrum and Sharp in press), I am able to assign this species to *Calycolpus*. A description of the species and reasoning for this generic assignment are given below.

***Calycolpus alternifolius*** (Gleason) Landrum, comb. nov.—*Myrtus alternifolia* Gleason, *Brittonia* 3:173. 1939.—TYPE: Venezuela, Bolívar, Auyan-tepui, 2200 m, *Tate 1344* (holotype, NY!).

Shrub to 2 m high, sometimes with trailing stems to 5 m long, the young growth mostly densely lanate to velutinous; hairs simple, to ca. 1.5 mm long, silvery-grey to yellowish-grey, straight or curled, spreading to ascending. Young twigs lanate, the hairs mainly persisting until the first bark falls, the older twig bark rough and cracked, light grey to blackish-grey, sometimes tinged with reddish-brown. Leaves opposite, or less often alternate, mostly separated by short internodes, elliptic, narrowly elliptic, obovate, ovate, or suborbicular, flat or revolute, 1.6–3.6 cm long, 0.6–2.5 cm wide, 1.4–3 (–4.6) times as long as wide, densely covered with hairs beneath, the upper surface tomentose in immature leaves, later glabrescent; apex acute to abruptly acuminate; base acute to rounded; petiole narrowly channeled, 1–3 mm long, 1–2 mm thick, lanate when young, losing most hairs with age; midvein impressed above, prominent below; lateral veins indistinct, or ca. 8–12 nearly straight, ascending pairs, scarcely visible, the marginal vein about equalling the laterals, about parallel to the margin; blades thickly coriaceous, drying olive-green to nearly black, lustrous above. Flowers pentamerous; peduncles 6–30 mm long, ca. 1 mm wide, solitary in the axils of leaves, uniflorous, densely lanate; bracteoles narrowly triangular to linear, 3–4 mm long, caducous at about anthesis; calyx-lobes triangular, 3–5 mm long, 1.5–3 mm wide, moderately pubescent within, lanate without; petals elliptic-obovate, 8–9 mm long, glabrous or with a ciliate margin; hypanthium lanate, obconic, 3–4 mm long; disk 2–4 mm across, tomentose; stamens 38–70, 3–5 mm long; anthers oblong, 0.8–1 mm long, with ca. 5–9 nearly equal glands in the connective; style ca. 5 mm long, glabrous to sparsely pubescent; ovary 2- to 3-locular; ovules 10–18 per locule, the placenta, a raised U-shaped pad. Fruit globose, tomentose, crowned with a persistent calyx, ca. 5–7 mm in diam.; seeds ca. 6, ca. 3 mm long, the seed coat lustrous, mostly 1 cell thick, the embryo whitish, C-shaped, the cotyledons not reflexed, accounting for less than  $\frac{1}{4}$  the embryo's length.

#### ANALYSIS OF RELATIONSHIPS

The characters of the following structures have been taken into account in my attempt to assign a generic position to *Myrtus alter-*



*nifolia*: 1) seed coat (surface; and outer seed coat thickness and prevalent cell shape in the outer seed coat); 2) embryo (cotyledon to hypocotyl ratio and cotyledons reflexed or not); 3) calyx-lobes (number and fusion); 4) anthers (shape, glandularity, and size in relation to the filament); and 5) vessel elements (with or without scalariform perforation plates).

*Seed coat.* In *Psidium* the seed coats a) are not lustrous but dull, b) have an external layer of pulpy tissue, c) have outer seed coats normally over 8 cells thick, and d) have outer seed coats in which the prevalent cell shape is elongate (Landrum and Sharp in press). *Myrtus alternifolia*, *Calycolpus*, *Mosiera*, *Myrteola*, and *Ugni* all differ in having seed coats that a) are lustrous, b) normally lack an external layer of pulpy tissue, c) have outer seed coats usually 1 to 4 cells thick, and d) have outer seed coats in which the prevalent cell shape is more or less isodiametric to oblong. These characters of the seed coat are the most useful in circumscribing *Psidium* and exclude *M. alternifolia* from the genus.

*Embryo.* The cotyledons of *Myrteola* and *Ugni* are about as long as the hypocotyl and are not reflexed. In the other genera and *Myrtus alternifolia* they are shorter than the hypocotyl; in *Psidium* and in some species of *Mosiera* and *Calycolpus* the cotyledons are reflexed. In *Myrtus alternifolia* they are not reflexed. Based on embryo structure then, *M. alternifolia* might belong to *Mosiera* or *Calycolpus*.

*Calyx-lobes.* *Mosiera* has 4 calyx-lobes, *Myrteola* has 4 or 5, and the rest of the genera and *Myrtus alternifolia* normally have 5. Thus, calyx-lobe number indicates that *Myrtus alternifolia* does not belong to *Mosiera*, but might belong to any of the other genera. Usually there is notable fusion of the calyx-lobes beyond the ovary's summit in *Psidium*, and there is often such fusion in *Calycolpus*. In *Myrtus alternifolia* and the other genera here considered, fusion is lacking. This character indicates that *Myrtus alternifolia* probably does not belong to *Psidium*.

*Anthers.* Anthers of most species of American Myrtaceae (including *Mosiera* and *Myrteola*) are subglobose and have no gland or a prominent terminal gland. In *Myrtus alternifolia*, *Calycolpus*, *Ugni*, and some species of *Psidium* the anthers are more or less elongate and have a few to several glands in the connective. In *Ugni* the mature filament is 1 to 3 times as long as the anther. In other species in this group the mature filament is more than 3 times as long as the anther. Thus, anther glandularity and proportional size indicate that *Myrtus alternifolia* should probably not be placed in *Mosiera*, *Myrteola*, or *Ugni*.

*Vessel elements.* In *Ugni* and *Myrteola* vessels have (or mostly have) scalariform perforation plates (Schmid and Baas 1984). *Myrtus*



*alternifolia* does not have scalariform perforation plates. One species of *Mosiera* (cited as *Psidium longipes* [O. Berg] McVaugh) and *Psidium pubifolium* Burret studied by Schmid and Baas were found to have simple perforation plates. The condition of other species of *Mosiera*, *Psidium*, and *Calycolpus* is not known to me. This character indicates that *Myrtus alternifolia* is not a member of *Ugni* nor *Myrteola*.

In summary *Psidium* is eliminated as a possible acceptor for *Myrtus alternifolia* because of seed coat characteristics. Elimination of *Ugni* and *Myrteola* seems warranted because of characters of the anthers, embryo, and vessel elements. *Myrtus alternifolia* would be out of place in *Mosiera* because of the glandularity of the anthers and calyx-lobe number. *Calycolpus* is not eliminated by any characteristic considered and the addition of *Myrtus alternifolia* does not add greatly to its variability.

Moreover, *Myrtus alternifolia* has leaves that are thickly coriaceous, and although the venation is faint, it can be seen to consist of several nearly straight lateral veins that connect with a discrete marginal vein. This is the common leaf type in *Calycolpus*.

Another factor that favors placing *Myrtus alternifolia* in *Calycolpus* is that it grows on the mountain peaks (tepui) of the Guayana highlands, the area in which *Calycolpus* is most diverse. *Mosiera*, perhaps the second most suitable acceptor for *Myrtus alternifolia*, is a Caribbean and Central American genus.

#### RECHARACTERIZATION OF *CALYCOLPUS*

Until now *Calycolpus* has been thought to be morphologically a rather uniform group, recognized by characteristics of the inflorescence (flowers usually borne in pairs on short axillary shoots), calyx ("open in bud and flower, with 5 broad and often flaring lobes"), and ovary (4- to 5-locular) (McVaugh 1968). Recent studies of *Calycolpus* indicate that none of these characteristics is as consistent as was previously thought and that seed coat and embryo characters indicate a somewhat more inclusive group than was accepted by McVaugh. In addition to *Myrtus alternifolia*, I would also include in *Calycolpus*, *Psidiopsis moritziana* Berg, which McVaugh (1956) placed in *Psidium*.

Even without *Myrtus alternifolia* and *Psidiopsis moritziana* there has been no particular characteristic found in all species of *Calycolpus* that is not also found in other genera. *Calycolpus*, at least at present, must be defined by a set of characters: seed coats lustrous, with no pulpy covering, the outer seed coat 1–4 cells thick with the prevalent cell shape more or less isodiametric; cotyledons shorter than the hypocotyl, reflexed or not; calyx-lobes normally 5, fused



or not beyond the ovary's summit; anthers elongate, with a few to several glands in the connective, about  $\frac{1}{3}$  to  $\frac{1}{10}$  as long as the filament; vessel elements with simple perforation plates. The following is an updated description of *Calycolpus* based on studies of the following species: *C. alternifolius*, *C. calophyllus* (Kunth) O. Berg, *C. cochleatus*, *C. goetheanus* (DC.) Berg, *C. legrandii* Mattos, *C. moritzianus* (O. Berg) Burret, *C. revolutus* (Schauer) O. Berg, *C. roraimensis* Steyerf., *C. surinamensis* McVaugh, and *C. warszewiczianus* O. Berg.

CALYCOLPUS O. Berg, Linnaea 27:378. 1856. Lectotype species: *C. goetheanus* (DC.) O. Berg. Designated by Riley (1926).

Shrubs or trees up to 10(–15) m high. Hairs whitish or yellowish, unicellular, simple or dibrachiate, up to ca. 1.5 mm long. Leaves persistent, coriaceous, the venation brochidodromous, with several pairs of nearly straight lateral veins that are united by a marginal vein that parallels the leaf margin. Inflorescence a solitary axillary flower or a very short axillary bracteate shoot with 1–3 decussate pairs of flowers. Flowers pentamerous (sometimes tetramerous in one population of *C. cochleatus*); calyx-lobes often flared, often with an apical appendage, the calyx fused beyond the ovary's summit and tearing between the lobes at anthesis or the calyx-lobes free; petals slightly fleshy, white or tinged with red, often drying brown; bracteoles usually small, about triangular, caducous at about anthesis or in *C. legrandii* leafy and persistent; stamens 35–270, folded centerward or more or less erect in the bud; anthers somewhat to markedly elongate, with about 4 to 40 glands; ovary 2- to 6-locular, the locular wall sometimes glandular; ovules 8–32(–ca. 80 in *C. moritzianus*), the placenta a U-shaped pad or mound of tissue or an essentially round peltate structure. Fruit subglobose; seeds few to numerous, about reniform, the seed coat hard, lustrous, the external wall 1–4 cells thick, the surface cells rounded to elongate, the central portion of the seed sometimes soft; embryo oily, whitish, C-shaped, the cotyledons reflexed or straight, less than  $\frac{1}{4}$  the length of the embryo.

#### ACKNOWLEDGMENTS

Special thanks go to Bruce Holst who sought out a specimen of *Calycolpus alternifolius* with mature seeds on the Auyan-tepui in Bolívar, Venezuela. I am also grateful to the curators of the following herbaria for allowing me to include their collections in my studies of *Calycolpus*: A, ASU, CAS, GH, MICH, MO, NY, UC, and US. Bruce Holst, David Keil, Rudolph Schmid, and Al Gentry offered helpful suggestions as to how this paper could be improved.

#### LITERATURE CITED

- BYRNES, N. 1982. The genus *Myrtus* or *Austromyrtus* in Australia? Austral. Syst. Bot. Newslett. 31:10–11.



- LANDRUM, L. R. and W. P. SHARP. 1989. Seed coat characters of some American Myrtinae (Myrtaceae): *Psidium* and related genera. Syst. Bot. 14 (in press).
- McVAUGH, R. 1956. Tropical American Myrtaceae. Notes on generic concepts and descriptions of previously unrecognized species. Field Mus. Nat. Hist., Bot. Ser. 29(3):145-228.
- . 1968. The genera of American Myrtaceae—an interim report. Taxon 17: 354-418.
- . 1969. Myrtaceae. In The Botany of the Guayana Highland—Pt. 8. Mem. New York Bot. Gard. 18(2):55-286.
- RILEY, L. A. M. 1926. Revision of the genus *Calycolpus*. Kew Bull. 1926:145-154.
- SCHMID, R. and P. BAAS. 1984. The occurrence of scalariform perforation plates and helical vessel wall thickenings in wood of Myrtaceae. Int. Assoc. Wood Anat. Bull. 5(3):197-215.
- SCOTT, A. J. 1979. New species and combinations in Myrtaceae from Malesia and Australia. Kew Bull. 33:511-515.

(Received 21 Jun 1988; revision accepted 25 Oct 1988.)



# TAXONOMIC RELATIONSHIPS OF *GILIA MACULATA* (POLEMONIACEAE)

ROBERT PATTERSON

Department of Biology, San Francisco State University,  
San Francisco, CA 94132

## ABSTRACT

*Gilia maculata* is reassigned from its previous placement in *Linanthus*. It was described originally by Parish in 1892 as *Gilia maculata*, and placed in *Linanthus* by Milliken (1904). This species is poorly known because of its rarity and because of its very small size, causing it to be easily overlooked in the field. Rediscovery of a population of *G. maculata* provided the opportunity to study this taxon critically. Leaf arrangement and shape, indumentum, corolla and calyx morphology, and pollen exine morphology, argue against its unequivocal assignment to *Linanthus*, and favor its inclusion in *Gilia*.

*Gilia maculata* Parish (Fig. 1) is a systematic enigma. It is a minuscule, little-known desert annual that occurs near the western margins of the Little San Bernardino Mountains of southern California (Fig. 2). It has been regarded by most floristic treatments as *Linanthus maculatus* (Parish) Milliken, although it has few diagnostic features of *Linanthus*. Although botanists and governmental agencies have sought it because of its potentially rare status, it has seldom been seen or collected, and few specimens are present in herbaria, making study extremely difficult. Furthermore, its relationships with other species of *Linanthus* or *Gilia*, as well as with other Polemoniaceae, have never been examined critically. In April 1986, a substantial population of this species was located near the northwest entrance to Joshua Tree National Monument, providing enough material to conduct a more thorough study of the morphological relationships of this species.

## TAXONOMIC HISTORY OF *GILIA MACULATA*

Parish's (1892) original description of *G. maculata* was as follows: "Inch high, diffusely branched from the base, sparsely pubescent; leaves entire, two lines long, broadly linear, thick and strongly carinate, obtuse, acerose; earlier flowers nearly sessile in the lower forks, later ones crowded above; calyx lobes nearly equal, much like the leaves but with a narrow hyaline membrane, ciliate; the narrowly campanulate tube of the corolla not exceeding the calyx, the limb rotate, two lines wide; filaments inserted on the base of the tube; anthers exserted; seeds few". Parish noted that the species was "... near *G. demissa* Gray, from which it differs in its entire leaves, obtuse



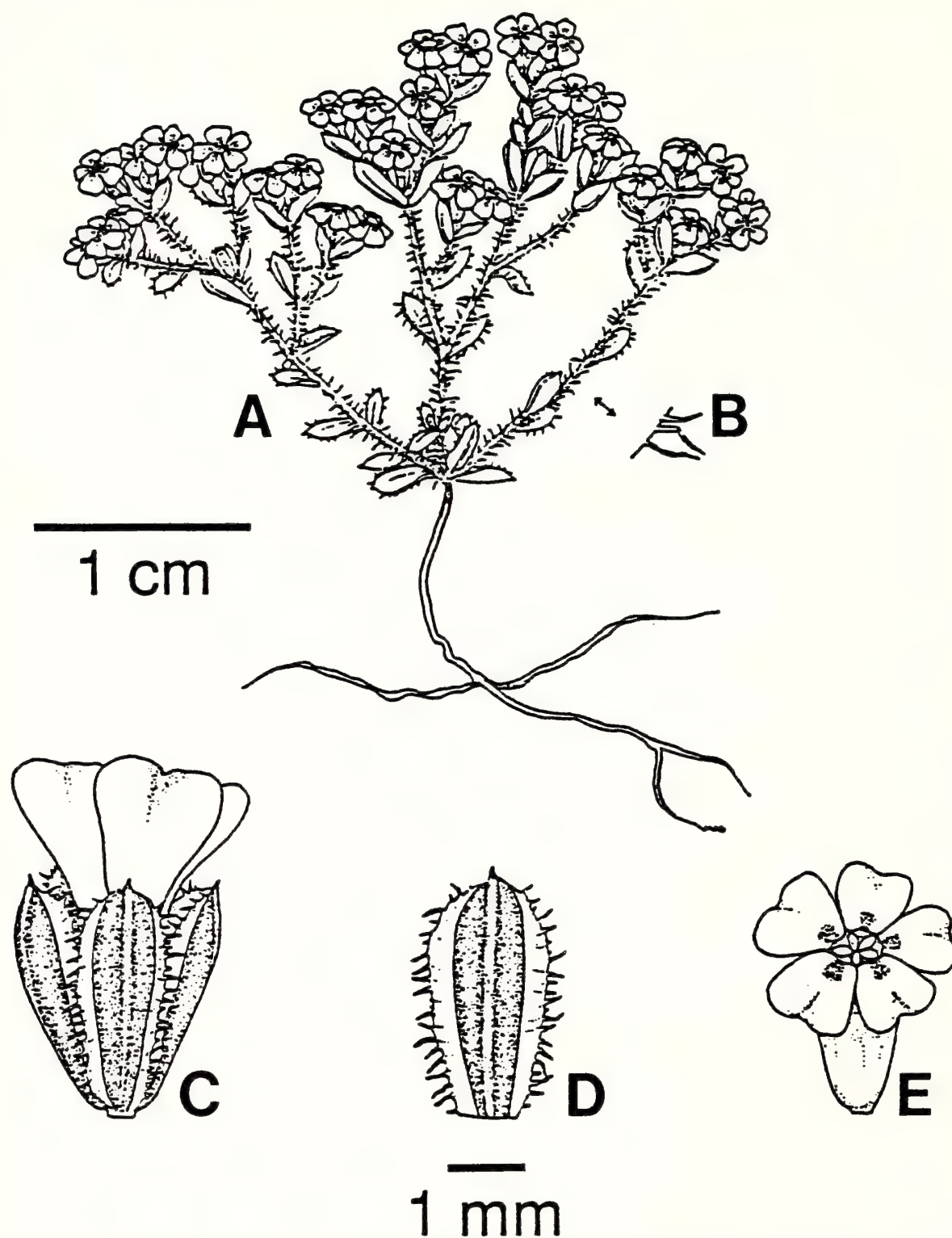


FIG. 1. *Gilia maculata*. A. Habit. B. Enlargement of trichomes. C. Flower at early anthesis. D. Calyx lobe showing hyaline margins. E. Face view of flower showing position of spots at base of corolla lobes.

and ciliate calyx-lobes, narrower corolla, and exserted anthers". The implication is that Parish considered the two species related based on an overall resemblance. It is not surprising that Parish did not recognize the new species as a member of *Linanthus*, because at that time most species recognized currently as *Linanthus* were included



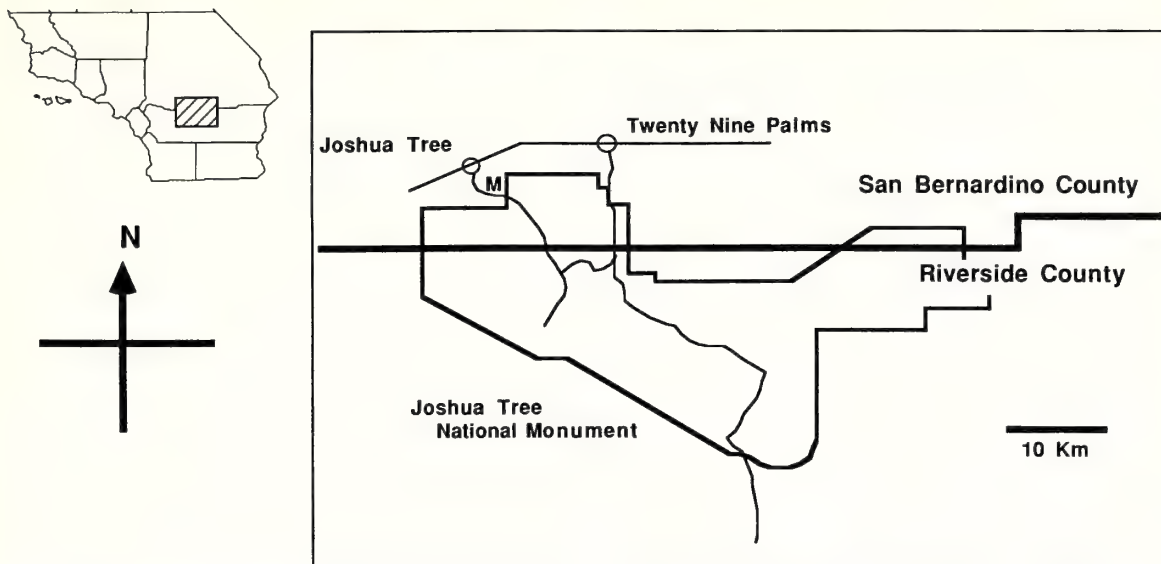


FIG. 2. Location of 1986 collection (M) of *Gilia maculata* (Bourell et al. 3000).

in *Gilia*. Although the genus name *Linanthus* dates from 1833, its common use did not begin until Greene's (1892) treatment.

Parish's original description is not completely in accord with the holotype or with material collected in the field during this study. Contrary to his description, the leaves of the holotype are, in fact, obovate and certainly not acerose (it is possible that Parish was referring to a mucronate tip, which may be present in some specimens). Parish also omitted certain other features that distinguish *G. maculata* from other genera in the family. He neglected to state in his description that the leaves of this taxon were alternate. He did, however, describe the calyx lobes as ciliate, identifying an important character that sets *G. maculata* off taxonomically.

Milliken (1904) placed this species in *Linanthus*, although without any explicit justification. Moreover, her description of *L. maculatus* is not in complete accord with her inclusive description of the genus *Linanthus*. She described the leaves of *L. maculatus* as "... entire, the upper sometimes alternate, oblong ...", whereas her description of the leaves for the genus reads "... opposite and palmately parted, or rarely entire and linear". Thus, although Milliken's treatment dictated the taxonomic status under which this species has been recognized in all modern floras, it failed to distinguish this species clearly as a member of *Linanthus*. If, in fact, Milliken's key to genera of Polemoniaceae were used, *G. maculata* would be identified clearly as a member of *Gilia*.

Brand's (1907) concept of *Gilia* included most of the tribe Gilieae, including *Linanthus*. He recognized *G. maculata* as a member of sect. *Campanulastrum*, along with *G. parryae* and *G. bella* (= *Linanthus p.* and *b.*), *Gilia dactylophyllum* (= *L. demissus*), and three currently recognized species of *Gilia*, *G. campanulata*, *G. filiformis*, and *G. micromeria*. This treatment is particularly noteworthy be-



cause it is the earliest occasion where *G. maculata* is allied with *G. campanulata*. Phenetically *G. maculata* is probably most closely related to *G. campanulata*, although there are still substantial differences that distinguish them. Grant (1959) later combined sect. *Campanulastrum* with sect. *Giliastrum* under the latter name, although without providing justification.

Subsequent treatments continued to recognize this taxon as *Linanthus* without apparent concern for accuracy of the taxonomic placement. Jepson (1925, 1943) recognized *L. maculatus* but did not refer directly to its alternate leaves. Only in the genus description did he allude to *Linanthus* as having leaves "rarely with some uppermost alternate". Interestingly, in his Manual (1925) he placed *L. maculatus* with *L. demissus* and *L. parryae* in subgenus *Parrya*. Later, in his Flora of California (1943) Jepson included *L. bellus*, *L. concinnus*, and *L. dianthiflorus* in this subgenus, circumscribing what Grant (1959) later referred to as sect. *Dianthoides*. It is noteworthy that Jepson (1943) made a special comment in the generic description that *L. maculatus* (among other species) has entire leaves. He also commented on the narrow endemism shown by the range of *L. maculatus*. It is curious that, with the extra attention given to this species in his Flora, Jepson did not discuss the significance of alternate leaves in this species.

Mason omitted *L. maculatus* from the entire treatment of the Polemoniaceae in Abram's illustrated Flora of the Pacific States (1951). It is unclear whether this was an oversight, or whether it was due to a belief on Mason's part that this species did not belong in *Linanthus*. Munz (1959, 1974) included *L. maculatus* in his treatments, describing it accurately as having alternate leaves, but making no other special mention of this character.

Because this species is not well known, and because the original diagnosis is scanty and not in complete agreement with the holotype material, an updated description is provided here based on material from the population collected in 1986:

***Gilia maculata*** Parish, Bull. Torrey Bot. Club 19:93. 1892. (figs. 1, 3).—*Linanthus maculatus* (Parish) Milliken, Univ. Calif. Publ. Bot. 2:55. 1904.—TYPE: USA, California, Riverside Co., borders of the Colorado Desert, at Agua Caliente [Palm Springs], *W. G. Wright s.n.* (holotype: CAS!).

Diminutive ephemeral annual 1–3 cm high. Stems branching above the first 1 or 2 leaves, densely hairy with 1- to 4-celled trichomes throughout. Leaves alternate, fleshy, narrowly oblanceolate or oblong, sessile, mucronate, marginally ciliate with 1- to 2-celled, white hairs from the base to at least  $\frac{1}{2}$  the length (often farther), the blade concave adaxially. Flowers borne in simple or compound cymes, sessile or subsessile, peduncle <1 mm long; calyx lobes narrowly



oblanceolate or spatulate with mucronate tip, ca. 2 mm long, green, distinct nearly to base (only the adjacent membranes connected at base), glabrous, with membranous ciliate margins extending to the tip, the trichomes 2(–3) cells long, the terminal cell long-acuminate (Fig. 1B); corolla campanulate, tube ca. 1.5–2 mm long, yellow or yellow-green, slightly hairy on inner surface, throat <1 mm long, white, lobes broadly ovate-cordate, tips slightly concave, 1–1.5 mm long, white with cerise spot at base, spreading at right angle to the tube or (more commonly) reflexed, venation simple, open; stamen filaments attached to near base of corolla tube, narrowly lanceolate, 1.5–2 mm long; anthers oval, slightly exserted beyond corolla throat; pollen yellow, round, exine reticulate with 10–12 slit-like apertures distributed evenly on the surface of the grains; ovary triangular-ovate, ca. 0.5 mm long, style 1 mm long, stigma lobes <0.5 mm long. Seeds minuscule, dark reddish-brown, non-mucilaginous, 10–12 per capsule,  $\pm$ distributed evenly among locules;  $n=9$ .

*Additional specimens.* USA, CA, San Bernardino Co., rd from Joshua Tree to Joshua Tree Natl. Mon., ca. 3.5 km S of junction with CAL Hwy 62, 6 Apr 1986, *Bourell, Patterson, and Timbrook 3000* (CAS); Coyote Holes, Joshua Tree National Monument, near line of Riverside and San Bernardino counties, 20 Apr 1924, *Munz 7941*; Chipmunk Trail, 28 Mar 1968, *Stebbins 6650* (CAS!); 17 mi W of 29 Palms on rd to Morongo Valley, 950 m, 6 Apr 1937, *Daniels s.n.* (CAS!); ca. 5 mi N of Windmill Tank, 3600 ft, 2 Apr 1942, *Ripley and Barneby 4273* (CAS!); 8 mi W of 29 Palms, 12 Apr 1935, *Keck 3843* (CAS!).

*Distribution and ecology.* *Gilia maculata* occurs in moderately coarse sand in open areas of *Larrea–Yucca brevifolia* scrub as a member of the annual spring flora. It is extremely inconspicuous in its gray-green herbage and white corollas, and blends well with the substrate, even when in flower (Fig. 3). It is likely that this may be one reason why the species is so little known in the field and poorly represented in herbaria.

The population that was rediscovered in April 1986 occurs at 1000 m elevation. No other populations were found during this study. It remains uncertain as to whether this population is representative of other populations of this species; however, considerable area of similar habitat occurs throughout the region. The Joshua Tree population consisted of approximately 100 individuals in April 1986; the following year the population was reduced markedly in number, but individuals were found in the same area.

*Relationships.* The decision to place *G. maculata* into one of the currently recognized genera of Polemoniaceae or to erect a new genus must be weighed carefully. Any decision is completely dependent





FIG. 3. *Gilia maculata* in the field. Note size compared with coin.

on how well the existing genera are known taxonomically. The Polemoniaceae have been studied carefully by many authors, but systematic and ecological relationships among most members of the family are not well understood. Although *G. maculata* is most commonly included as a member of *Linanthus*, even superficial consideration of morphological characters does not support this alignment. The most commonly used defining feature for the genus *Linanthus* within the Polemoniaceae has been the presence of opposite leaves that are either a) palmately-divided with linear or narrowly lanceolate divisions or b) entire and linear. Presumably the entire leaves in certain species (e.g., *L. dichotomus* and relatives, *L. dianthiflorus*) represent a reduction of leaf lobes to one. *Linanthus* sensu stricto never has completely alternate leaves, although occasionally in some species the upper leaves near the inflorescence are subopposite. Inclusion of *G. maculata* as a member of *Linanthus* is out of accord with the morphological unity of the latter; it would be difficult to distinguish *Linanthus* as a discrete genus were *G. maculata* included. Bentham (1833), Greene (1892), and Milliken (1904), as well as nearly all subsequent authors, recognized the taxonomic importance of leaf morphology in this lineage, and I find no reason to diminish its value.

In addition to having alternate arrangement, the oblong-obovate



leaves of *Gilia maculata* represent a shape not found in any other species of *Linanthus*. This character appears to have been neglected as a distinguishing feature, although it is mentioned in several descriptions of the species (Jepson 1925, 1943; Munz 1959, 1974). Most species of *Linanthus* have linear or linear-lanceolate leaf lobes or leaves. The only species of *Linanthus* that have oblanceolate leaf lobes are in sect. *Leptosiphon* (e.g., *L. oblanceolatus*, *L. bicolor*); however, other morphological differences (corolla shape, leaf arrangement and divisions, inflorescence structure) between this section and *G. maculata* are so strong that similarity in leaf or leaf lobe shape can be regarded as an example of convergence.

Not only is the placement of *G. maculata* in *Linanthus* difficult based on the circumscription of the latter genus, there is no apparent morphological alliance between the former species and any existing species of *Linanthus*. Previously suggested relationships with other species of *Linanthus* are problematic. Parish (1892) and Jepson (1925, 1943) proposed an alliance with *L. demissus* (sect. *Dianthoides*) presumably founded on a superficial resemblance in habit and corolla morphology. Although both taxa are small desert annuals with white campanulate corollas with reddish basal spots on the lobes, other features do not support a close relationship. Pollen exine patterns of these two species are strikingly different (Fig. 4), and provide convincing evidence against a taxonomic alliance. *Linanthus demissus* has striate regions amid a reticulate exine, a pattern characteristic of certain species of *Linanthus* sect. *Dianthoides*. *Gilia maculata* lacks any striations and is uniformly reticulate, a pattern that occurs in certain species of *Gilia* and in most other *Linanthus* species. Inasmuch as pollen exine patterns have been extremely useful in helping to understand relationships in the Polemoniaceae (Stuchlik 1967a, b; Taylor and Levin 1975; Chuang et al. 1978; Day and Moran 1986; Timbrook 1986; Patterson, Golden, and Vagenas, unpubl.), this divergence suggests a strong taxonomic difference. Irrespective of relationships between *G. maculata* and other *Gilia* species as indicated by pollen morphology, taxonomic placement of *G. maculata* near *L. demissus* is not defensible. Additionally, *L. demissus* has palmately divided, opposite leaves (although upper leaves may occasionally be subopposite, the majority of the leaves remain opposite).

Other species within sect. *Dianthoides*, in which *G. maculata* was placed by Grant (1959), share few if any diagnostic characters with the latter species. Only *L. dianthiflorus* has simple leaves, but these are linear and opposite. Deeply cleft calyx tubes are present in *L. parryae*, *L. bellus*, and *L. demissus*, but they are not as deeply cleft as in *G. maculata*—there is always a fused portion, i.e., a calyx tube. Leaves of *L. bellus* and *L. parryae* are always opposite and palmately cleft.

One feature shared by *G. maculata* and most members of sect.



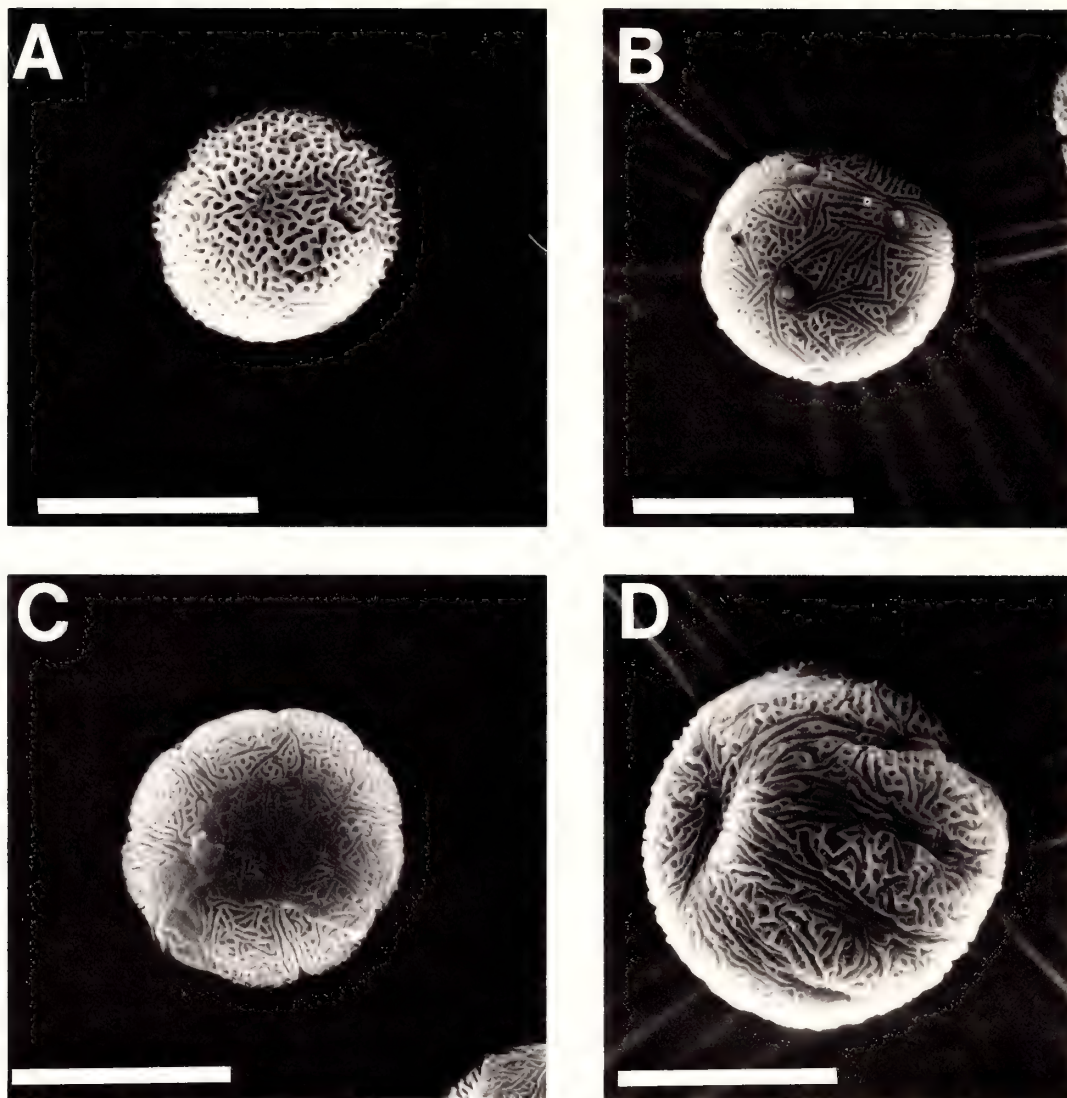


FIG. 4. Scanning electron micrographs of pollen grains. A. *Gilia maculata*. B. *Linanthus demissus*. C. *G. campanulata*. D. *G. inyoensis*. Bar represents 20  $\mu$ m.

*Dianthoides* is the presence of red marks at the base of the corolla lobes. In this respect the corolla of *L. demissus* is similar superficially to that of *G. maculata*; however, it is likely that this represents convergence in corolla color pattern. Presence of red spots on corolla lobes is common in many species of *Linanthus*, and is present as a character in sects. *Pacificus* and *Leptosiphon*, as well as in *Dianthoides*. An argument in support of corolla color pattern as indicative of close relationship in this case negates the importance of other features such as leaf arrangement and shape. The latter characters have had a major role in distinguishing genera within the family, but corolla color patterns have rarely been regarded as important generic diagnostics. As Grant (1965) points out, although evolution of floral morphology (including color patterns) has been a major factor in speciation in the Polemoniaceae, it is apparent that similar color patterns have evolved more than once across generic lines.

*Gilia* is the only genus in which *G. maculata* can readily be incorporated based on comparative morphology. *Gilia* is a large, mor-



phologically diverse, polythetic genus. Its circumscription is difficult, and it is most easily recognized by lacking characters that are present in other genera. Leaves are always alternate in *Gilia*, but leaf, trichome, and floral morphology in *Gilia* is extremely diverse. The basic chromosome number in the genus is  $x=9$ , as it is for *Linanthus* (Grant 1959; Patterson 1979).

*Gilia* was partitioned into five sections (Table 1) by Grant (1959), each of which is morphologically and ecologically diverse. *Gilia maculata* has morphological features that ally it with members of sect. *Giliastrum* Brand. This section ranges from perennials such as *G. ripleyi* to diminutive annuals like *G. campanulata* and *G. inyoensis*. It is also poorly understood from a taxonomic viewpoint (Grant 1965). One character that distinguishes it from other sections of *Gilia* is the presence mostly of campanulate or rotate corollas. This feature is present not only in *G. maculata*, but also in three other small desert annuals: *G. campanulata*, *G. inyoensis*, and *G. tenerrima*.

Another character by which these four species are allied is calyx morphology. The calyx is divided into five lobes to near the base (the lobes actually appearing distinct), with membranous margins that extend most to all of the length of the calyx lobes (Fig. 1D). This feature is absent in other species of *Gilia*.

Pubescence features also appear to ally these species while illustrating the complex interrelationships among them. All four species are moderately to densely pubescent on their stems, leaves, and calyx lobes. The trichomes are generally 2- to 4-celled long, and uniseriate. They show a further similarity among these species in that cells appear to alternate in orientation with respect to one another, forming a "chain link" structure (Fig. 1B). Slightly different trends in cell number exist among different species and on different organs, but irrespective of these differences, trichome morphology provides an additional argument for including *G. maculata* within sect. *Giliastrum*.

Despite similarities among *Gilia maculata* and the other three species cited above, it is notably distinct in other characters. In particular, no other species of *Gilia* have ciliate leaf margins and calyx lobes. Furthermore, the pollen exine pattern of *G. maculata* is different from that of any other *Gilia* species, especially that of *G. campanulata* or *G. inyoensis* (Fig. 4). Pubescence type and pollen exine morphology are regarded generally as conservative characters and have been used in numerous instances as taxonomically valuable characters throughout the Polemoniaceae (Grant 1959; Patterson 1977; Timbrook 1986; Gordon-Reedy in press). Therefore, although affinities exist between *G. maculata* and certain other species of sect. *Giliastrum*, strong differences remain, rendering the problem of relationships with the remainder of the genus far from solved.



TABLE 1. FEATURES OF THE FIVE SECTIONS OF *GILLIA* (SENSU GRANT 1959).

|               | <i>Giliastrum</i><br>(including <i>G. maculata</i> ) | <i>Giliandra</i>           | <i>Gilia</i> | <i>Arachnion</i> | <i>Saltugilia</i>                    |
|---------------|--|----------------------------|--------------|------------------|--------------------------------------|
| Duration      | Annuals and perennials                               | Annuals and perennials     | Annuals      | Annuals          | Annuals                              |
| Lower leaves  | Mostly not deeply lobed                              | Once-pinnate               | 1-3 Pinnate  | 1-3 Pinnate      | 1-3 Pinnate or linear                |
| Upper leaves  | Similar to lower leaves                              | Reduced                    | Reduced      | Very reduced     | Reduced or well-developed and entire |
| Corolla shape | Campanulate or rotate                                | Funnelform                 | Funnelform   | Funnelform       | Funnelform                           |
| Pollen color  | Yellow or blue                                       | Mostly yellow, rarely blue | Blue         | Blue             | Blue                                 |



*A case for and against a new genus.* It is inevitable that, as more taxonomic information has become available in the Polemoniaceae, reassessments have appeared, often necessitating recognition of new taxa above the level of species. Day and Moran (1986) recently accumulated evidence in favor of reassigning the former *Ipomopsis gloriosa* to a new genus, *Acanthogilia*; the combination of characters in this taxon precluded unequivocal placement in any previously existing genus. Timbrook (1986) similarly reaffirmed the generic status of *Loeseliastrum*, formerly a section of *Langloisia*. A strong case might be made for a similar treatment of *G. maculata*, inasmuch as it does not ally very closely with any known member of *Gilia*, and certainly not with *Linanthus* or any other existing genus in the family. Morphologically it represents a mosaic of features from different genera, lacking all of the defining characters of even the more variable genera in the family. However, a large number of unsolved questions remain about relationships within *Gilia* as well as among *Gilia* and other genera. Other genera in the Gilieae are reasonably well-circumscribed and distinct, even though they may share a suite of characters with *Gilia*. Based on information presently available, *Gilia maculata* does not possess any character or combination of characters that clearly set it apart at the generic level. Further studies of character distribution in this species and in the remaining species of *Gilia* may provide an alternative insight on this problem.

*Taxonomic importance of *Gilia maculata*.* Questions of evolutionary and taxonomic importance remain in which *G. maculata* may provide some insight. Its previous placement within and without *Linanthus* reemphasizes the point that there is a great deal that is not understood clearly about the relationship between *Linanthus* and *Gilia*. For example, just as *G. maculata* has been moved from *Linanthus* in this study, Moran (1977) removed *L. uncialis* from *Gilia*. In neither case are morphological features problematic or difficult to measure; rather, both of these species are poorly known, being uncommon and inconspicuous in the field, and poorly represented in herbaria. This underscores the need for considerable caution in assessing taxonomic relationships when some or all members of a group are not completely understood. It is also noteworthy that both of these species have been placed in *Linanthus* sect. *Dianthoides* and *Gilia* sect. *Giliastrum*. This situation suggests that an evolutionary connection between *Gilia* and *Linanthus* might be sought among these two sections. Such an hypothesis is attractive in exploring further the relationships between these genera. The position of *G. maculata* in the California flora also remains unknown. Its isolation in the Little San Bernardino Mountains, a region not particularly well-associated with isolated and endemic plant species, is not readily explained; neither is its geographic disjunction



by over 300 km from its postulated nearest relatives, *G. inyoensis* and *G. campanulata*. In addition, not only is there minimal information about population size in this species, but virtually nothing is known about its reproduction (e.g., pollination, seed production, dispersal). Prior to attempting to answer questions about evolution in this species, considerably more information must be gathered regarding the ecology, distribution, and reproductive biology of *G. maculata*.

#### ACKNOWLEDGMENTS

Thanks are due to the following persons: Mona Bourell and Steve Timbrook for helping to find *G. maculata* in the field and for valuable discussions; Mary Ann Showers and Rich Simpson for preparation of figures; Ginger Vagenas for SEM assistance; Peggy Fiedler for reviewing an early draft of the manuscript; and especially to Alva Day for her thoughtful consult and help in interpreting relationships within *Gilia*. Part of this work was facilitated by a SFSU Professional Research and Development Award.

#### LITERATURE CITED

- BENTHAM, G. 1833. Polemoniaceae. Bot. Reg. 19:t. 1622.
- BRAND, A. 1907. Polemoniaceae. A. Engler, Das Pflanzenreich 4 (250).
- CHUANG, T., W. C. HSIEH, and D. H. WILKEN. 1978. Contribution of pollen morphology to systematics in *Collomia* (Polemoniaceae). Amer. J. Bot. 65:450–458.
- DAY, A. G. and R. MORAN. 1986. *Acanthogilia*, a new genus of Polemoniaceae from Baja California, Mexico. Proc. Calif. Acad. Sci. 44:111–126.
- GORDON-REEDY, P. 1989. Trichome patterns and geographic variation in *Leptodactylon californicum* (Polemoniaceae). Madroño (in press).
- GRANT, V. 1959. Natural history of the *Phlox* family: systematic botany. M. Nijhoff, The Hague.
- . 1965. Flower pollination in the *Phlox* family. Columbia Univ. Press, New York.
- GREENE, E. L. 1892. Some American Polemoniaceae. Pittonia 2:251–260.
- JEPSON, W. L. 1925. A manual of the flowering plants of California. A.S.U.C. Bookstore, Berkeley, CA.
- . 1943. Polemoniaceae. In A flora of California 3:131–222. A.S.U.C. Bookstore, Berkeley, CA.
- MASON, H. L. 1951. Polemoniaceae. In L. R. Abrams, Illustrated flora of the Pacific states 3:396–474. Stanford Univ. Press, Stanford, CA.
- MILLIKEN, J. 1904. A review of California Polemoniaceae. Univ. Calif. Publ. Bot. 2:1–71.
- MORAN, R. 1977. New or renovated Polemoniaceae from Baja California, Mexico. Madroño 24:141–159.
- MUNZ, P. A. 1959. A California flora. Univ. California Press, Berkeley, CA.
- . 1974. A flora of southern California. Univ. California Press, Berkeley, CA.
- PARISH, S. B. 1892. New California plants. Bull. Torrey Bot. Club 19:93.
- STUCHLIK, L. 1967a. Pollen morphology in the Polemoniaceae. Grana Palynol. 7: 146–240.
- . 1967b. Pollen morphology and taxonomy of the family Polemoniaceae. Rev. Palaeobot. Palynol. 4:325–333.
- TAYLOR, T. N. and D. A. LEVIN. 1975. Pollen morphology of Polemoniaceae in



relation to systematics and pollination systems: scanning electron microscopy. *Grana* 15:91–112.

TIMBROOK, S. 1986. Segregation of *Loeseliastrum* from *Langloisia* (Polemoniaceae). *Madroño* 33:157–174.

(Received 9 Nov 1987; revision accepted 15 Oct 1988.)

## ANNOUNCEMENT

### RELOCATION OF UC AND JEPS TO INTERIM QUARTERS

During March and April 1989, the UC and JEPS collections will be temporarily relocated to a site several miles from the UC-Berkeley campus; the staff will move in May or June. The herbaria will be housed at the off-campus site until renovation of new quarters in the Life Sciences Building is completed at the end of 1992. Interim quarters will be fully functional and accessible to researchers. We expect to retain our phone numbers, and mail addressed to “University Herbarium” or “Jepson Herbarium” (but *not* “Department of Botany”) will be delivered to our new location.

The move is being coordinated in such a way as to minimize disruption of research needs. Loans will generally be unaffected, other than potential minor delays in processing. We do ask that shipments to UC of routine exchange, returned loans, and similar low-priority transactions be kept to a minimum until June 1989, so that our staff can concentrate on the move.

Visitors during March and April 1989 should contact us in advance to determine whether or not their groups have been moved, and what needs to be done to bring the researcher and specimens together. Except for the day or two that any group of specimens is in transit, they should be accessible at one place or the other, but special arrangements will need to be made to provide access to the new quarters until June 1989.

The location of the interim quarters is at 6701 San Pablo Avenue, two blocks south of Ashby Avenue at the junction of Berkeley, Oakland, and Emeryville. The herbaria will occupy a minor portion of a huge warehouse owned by the University, commonly referred to as the Merchant Building. The facility is easily accessed by automobile from Interstate Highway 80 at the Ashby Exit. For public transportation, take a bus from the Ashby BART Station west along Ashby Avenue to San Pablo Avenue.

Eastern Hemisphere collections of spermatophytes (except Asteraceae, Apiaceae, Myrtaceae, and Ranunculaceae) will continue to be housed at the annex established five years ago adjacent to campus. After renovation is complete, however, these collections will be reintegrated into the main herbarium. Until then, visitors who expect to see these specimens should make arrangements in advance.



*MACROMERIA ALBA* (BORAGINACEAE), A NEW SPECIES  
FROM TAMAULIPAS, MEXICO

GUY L. NESOM

Department of Botany, University of Texas,  
Austin, TX 78713

ABSTRACT

*Macromeria alba* is described from Gomez Farías area in the Sierra Guatemala of west-central Tamaulipas. It is most closely related to *M. notata* from the high mountains of Coahuila and Nuevo León to the north.

RESUMEN

Se describe *Macromeria alba* de la región de Gomez Farías en la Sierra Guatemala en la oeste-central de Tamaulipas. La especie nueva parece tener afinidades estrechas con *M. notata*, la cual se encuentra en las montañas altas del norte de Coahuila y Nuevo León.

Continued curation of the Boraginaceae at TEX-LL has brought to light an undescribed species of *Macromeria*. It is the second new borage from the Sierra Guatemala of west-central Tamaulipas (see Nesom 1988)—both made by Dr. Alfred T. Richardson, presently at Texas Southmost College in Brownsville. This species is the first addition to the genus since Johnston's revision (1954), making a total of nine currently recognized species. The genus ranges from the southwestern United States to Guatemala with two species-rich areas, one in northeastern Mexico and the other in southwestern Mexico.

***Macromeria alba*** Nesom, sp. nov. (Fig. 1)—TYPE: MÉXICO, Tamaulipas, Mpio. Gomez Farías, area W of Rancho del Cielo in the sierra, ca. 5–7 km NW of Gomez Farías, between San Jose and La Perra [just S of Agua del Indio, area of pine-oak], 30 May 1969, *A. Richardson 1263* (holotype, TEX).

*M. notatae* simile sed foliis brevipetiolatis, lobis calycis brevioribus, et corollis albis lobis multo longioribus differt.

Perennials to 2 m tall. Stems with ascending-appressed hairs 0.3–1.5 mm long. Leaf blades lanceolate-elliptic to ovate-lanceolate, 2.5–10 cm long, 8–30 mm wide, with primary veins slightly impressed above, raised beneath, lighter-colored beneath; apices acute to acuminate, bases obtuse to rounded and abruptly forming a stipe-like petiolar base 1–2 mm long, margins entire, usually narrowly revolute, appressed-ciliate; the lower surfaces evenly strigose with closely





FIG. 1. Habit of *Macromeria alba* (from Richardson 366).



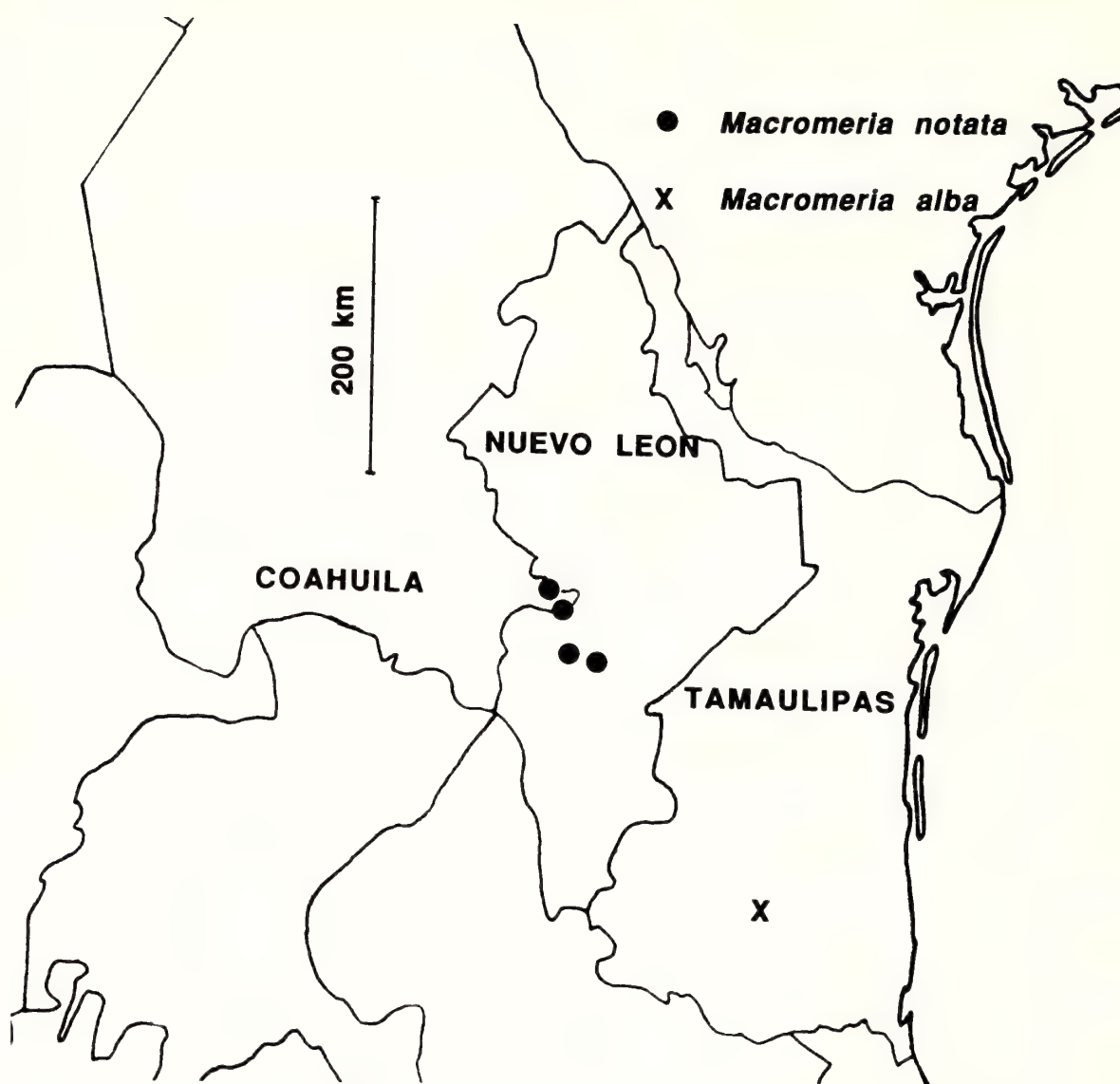


FIG. 2. Distribution of *Macromeria alba* and *M. notata*.

appressed hairs mostly 0.5–0.9 mm long, upper surfaces usually with minute, pustulate trichome bases without emergent trichomes, or trichomes, when present, never more than 0.2 mm long. Flowers in axils of well-developed leaves on internodes 5–10 mm long, mature fruits separated on internodes up to 40 mm long; pedicels 5–8 mm long in flower, to 13 mm long in fruit; calyx lobes linear-triangular, 0.5–1 mm wide, 6–8 mm long in flower, to 11 mm long in fruit; corollas white, prominently spreading-hairy on the outside, 42–47 mm long, gradually ampliate from near the base, regular, 4–6 mm wide (pressed) at the throat, lobes erect or ascending, lanceolate to ovate-lanceolate or triangular, 6–9 mm long, inner surface of each with a band of stipitate-glandular hairs beginning in the throat and extending halfway to the apex, corollas otherwise glabrous inside; style persistent, as long as or slightly longer than the filaments, barely exerted, stigma subterminal, separated by sterile tip of the style; anthers glabrous, 2 mm long, medio-fixed, filaments as long as the



corolla. Nutlets ovoid, smooth and shiny, white or brownish, 2 mm wide, 2.5–3 mm long.

Known only from the region of Rancho del Cielo near Gomez Farías, Sierra de Guatemala, Tamaulipas, at ca. 4800–6300 ft in elevation (Fig. 2).

PARATYPES: MEXICO, Tamaulipas, Mpio. Gomez Farías, area of Rancho de Cielo, ca. 5–7 km NW of Gomez Farías: Agua Linda trail, 5 Jun 1969, *Richardson 1367* (TEX); between Indian Springs and Agua Linda turnoff, 26 Jun 1968, *Richardson 366* (TEX).

*Macromeria alba* is clearly most similar to *M. notata* I. M. Johnston and keys to that species in Johnston's study (1954) of the genus. Both species have corollas with erect or ascending lobes and with prominent lines of stipitate glands (described in *M. notata* as "weakly invaginate elongate densely glanduliferous plaits") on each lobe extending from inside the throat below each lobe to beyond the middle of it. As noted by Johnston, *M. longiflora* D. Don and *M. pringlei* Greenman also have glandular corollas with erect lobes, although the glands are not positioned similar to those of *M. alba* and *M. notata*. The epithet "alba" refers to the corolla color (as noted by the collector); in the other species of *Macromeria*, corollas usually range from yellow to light yellow or yellow-green. Differences between the new species and its closest relative are presented in the following couplet.

- A. Stem pubescence of hairs variable in length, all ascending-appressed; leaves usually abruptly narrowed at the very base to a stipe-like petiole 1–2 mm long; pedicels 5–8 mm long in flower; calyx lobes 7–8 mm long in flower; corollas white, funnelform, gradually opened to the throat, the lobes 6–9 mm long, lanceolate to ovate-lanceolate. . . . . *M. alba*
- A. Stem pubescence a mixture of short, arching-appressed hairs and longer, straight, spreading ones; leaves basally attenuate and sessile, not at all petiolate; pedicels 2–4 mm long in flower; calyx lobes 10–15 mm long in flower; corollas yellow with greenish lobes, slightly funnelform, abruptly flaring at the throat, the lobes 3–5 mm long, widely to very widely ovate. . . . . *M. notata*

The pubescence of the upper leaf surface in *Macromeria alba* mostly consists of minute, pustulate bases without emergent trichomes, or when trichomes are present they are never more than 0.2 mm long. In *M. notata* the trichomes are 0.5–0.1 mm long. In *M. notata*, the flowers are tightly clustered at the branch tips, compared to the more distantly separated flowers and fruits of *M. alba*. In addition, label data indicate that plants of *M. alba* grow to a height of about 2 m, whereas the collections of *M. notata* are all of plants 0.2–0.5 m tall.

*Macromeria alba* apparently is endemic to the area just west of Gomez Farías in the Sierra Guatemala of west-central Tamaulipas. All collections were made in an area of pine-oak woodland (Al Richardson pers. comm.). *Macromeria notata* is a species apparently restricted to high mountains of Coahuila (Sierra de Viga) and Nuevo



León (Sierra Infernillo—the type, Sierra de la Marta, and Cerro Potosí). The closest known localities of the two species are about 200 kilometers apart.

#### ACKNOWLEDGMENTS

I greatly appreciate the helpful comments of Jim Miller and other reviewers.

#### LITERATURE CITED

- JOHNSTON, I. M. 1954. Studies in the Boraginaceae, XXVI. Further reevaluations of the genera of the Lithospermeae. *J. Arnold Arbor.* 35:1–81.  
NESOM, G. L. 1988. A synopsis of the American species of *Omphalodes* Tourn. (Boraginaceae). *Sida* 13:25–30.

(Received 5 Jul 1988; revision accepted 16 Nov 1988.)

---

### NOTEWORTHY COLLECTION

#### CALIFORNIA

**PRUNUS FASCICULATA** (Torrey) A. Gray var. **FASCICULATA** (ROSACEAE).—San Luis Obispo Co., E foothills of La Panza Mts. on hill above Domínez Rd between Del Rosa and Doris Trail in California Valley tract area, unit 32, T30S R19E, NW¼ of sect. 31, 645 m, ca. 80 individuals among rocks, assoc. with *Ericameria linearifolia* and grasses, 30 Mar 1988, *Douglas Chadwick s.n.* (OBI).

*Previous knowledge.* The desert almond is widespread in transmontane deserts of SE CA, and ranges E to NV, UT, and AZ. In CA it is occasional to locally abundant in desert portions of Transverse and Peninsular ranges, desert-facing slopes of the southern Sierra Nevada, and various of the transmontane desert ranges.

*Significance.* First record for S Coast Ranges of cismontane CA; disjunct by ca. 165 km from nearest population (in S Sierra Nevada near Onyx, Kern Co.; Twisselmann, Fl. Kern Co., Calif., 1967). *Prunus fasciculata* is represented in coastal areas of San Luis Obispo and Santa Barbara cos. by var. *punctata* Jepson, the sand almond, a taxon restricted to coastal dune formations (Hoover, Vasc. Pl. San Luis Obispo Co., Calif., 1970; Smith, Fl. Santa Barbara Region, Calif., 1976). The population of *P. fasciculata* var. *fasciculata* is separated from the nearest San Luis Obispo Co. populations of var. *punctata* by ca. 78 km and by the principal ridges of the La Panza and Santa Lucia Mts. In its hot, dry climate the California Valley and adjacent regions of the Carizzo Plain resemble the Mojave Desert much more than they do the coastal dune areas.—ANN CHADWICK and DAVID J. KEIL, Biological Sciences Department, California Polytechnic State University, San Luis Obispo, CA 93407.



TAXONOMY OF *STREPTANTHUS* SECT. *BIENNES*,  
THE *STREPTANTHUS MORRISONII* COMPLEX  
(BRASSICACEAE)

REBECCA W. DOLAN  
Holcomb Research Institute and  
Biological Sciences Department,  
Butler University, 4600 Sunset Avenue,  
Indianapolis, IN 46208

LAWRENCE F. LAPRÉ  
Tierra Madre Consultants, 4178 Chestnut Street,  
Riverside, CA 92501

ABSTRACT

The *Streptanthus morrisonii* complex is a six-taxon group of closely related serpentine rock outcrop endemics from Lake, Napa, and Sonoma counties of California, USA. Two new subspecies (*S. morrisonii* subsp. *kruckebergii* and *S. brachiatus* subsp. *hoffmanii*) from Lake County, California, are described. The relationship of these taxa to others in the section is reviewed and descriptions and a key are provided.

Floristic surveys of serpentine rock outcrops conducted for environmental impact reports for geothermal and gold-mining operations in Lake, Napa, and Sonoma counties of California, have revealed new data on many rare and unusual plants. During these surveys previously undescribed populations of plants were discovered that are clearly members of the section *Biennes* of the genus *Streptanthus* (the *Streptanthus morrisonii* F. W. Hoffman complex), and yet do not match the morphology or geographical distribution of the described taxa (Hoffman 1952). Some *Streptanthus* taxa restricted to serpentine are known for extreme local differentiation (Kruckeberg 1956, 1958). We undertook a study of the biochemistry, morphology, and distribution of the section to evaluate the existing taxonomy and to determine the taxonomic status of newly-discovered populations.

Hoffman (1952) first addressed the taxonomy of “biennial” (i.e., monocarpic perennial) *Streptanthus*. He collected and described two species, one with three subspecies. These plants grow on serpentine outcrops of limited access and had not previously been collected. Hoffman placed his taxa in the subgenus *Euclisia* Nutt. ex Torrey & A. Gray (*Streptanthus* with zygomorphic flowers, nonbracteate inflorescences, and one or two pairs of stamens with connate or partially connate filaments), that was monographed by Morrison in



1941. The biennial *Streptanthus* were recognized as section *Biennes* by Kruckeberg and Morrison (1983).

Members of the *Streptanthus morrisonii* complex have glabrous and glaucous vegetative parts. Their most distinctive feature is cabbage-like rosette leaves that are broad, palmately-lobed, fleshy or succulent, and often mottled on the adaxial surface. Succulent rosette leaves indicate the biennial life history characteristic of the group. Some related *Streptanthus* that grow on serpentine also possess fleshy rosette or basal leaves. This tendency toward succulence appears to be one of the suite of traits shared by serpentine endemics (Kruckeberg 1984a, b).

The newly discovered populations differ from the described taxa of the complex in morphological traits and/or geographic range. Plant habit, flower color, and leaf characteristics are the most significant discriminating traits. These features and genetic relationship as revealed by starch gel electrophoresis of enzyme variants (unpubl. data) support the taxonomy of the section as developed by Hoffman (1952) with the addition of two new subspecies; one each for *Streptanthus brachiatus* and *S. morrisonii*. The relationship of these subspecies to other members of the complex is presented in the following taxonomic treatment. Type localities for the taxa are mapped in Figure 1. Additional collection sites are in the immediate vicinity of the type localities for these extremely restricted endemics.

**STREPTANTHUS** Nutt. sect. **BIENNES** Kruckeb. & J. Morrison, *Madroño* 30:242. 1983.

Glaucous and glabrous biennials, low (20 cm) to tall (75–125 cm), the first year rosettes of petiolate, broadly spatulate, and coarsely dentate leaves. Flowers in openly branched racemes or panicles, zygomorphic; calyces flask-shaped; sepals glabrous or setose, yellow to purple, carinate; petals white to salmon-colored, crisped, unequal, recurved; stamens in 3 unequal pairs (upper, lateral, and lower), the upper with connate filaments, strongly recurved upward, the lower set partially connate and recurved downwards. Siliques erect, divaricate or reflexed, usually torulose; seeds only weakly winged at tip; cotyledons accumbent.

#### KEY TO TAXA OF SECTION *BIENNES* OF *STREPTANTHUS*

- A. Plants short (10–30 cm) and much branched near the base. . . . 1. *S. brachiatus*
  - B. Calyces glabrous, rose-purple; endemic to the immediate vicinity of Socrates Mine, Sonoma County. . . . . 1a. *S. brachiatus* subsp. *brachiatus*
  - B. Calyces usually pubescent, yellow or dark purple; endemic to the Sulphur Creek drainage on Lake/Sonoma county line. . . . . 1b. *S. brachiatus* subsp. *hoffmanii*
- A. Plants tall (30–100 cm) and remotely branched. . . . . 2. *S. morrisonii*
  - C. Calyces densely pubescent with long (2 mm) hairs, dark purple; endemic to the headwaters of East Austin Creek, Sonoma County. . . . . 2a. *S. morrisonii* subsp. *hirtiflorus*



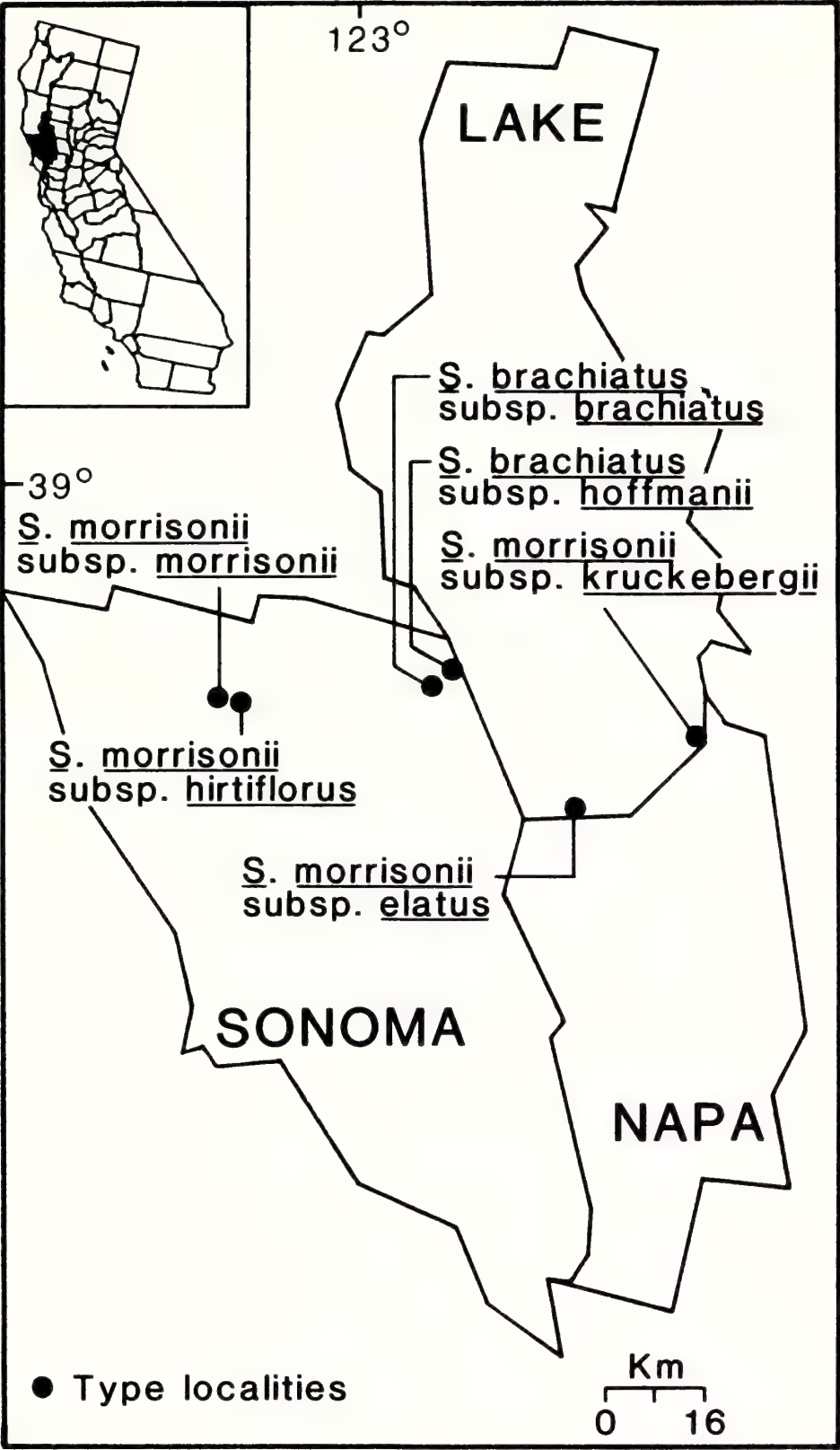


FIG. 1. Map of type localities of the *Streptanthus morrisonii* complex.

- C. Calyces glabrous to slightly pubescent, greenish yellow to golden yellow.
- D. Upper and lower surfaces of rosette and lower cauline leaves usually green; upper connate filaments uniformly orange or orange-yellow; endemic to drainage of Big and East Austin creeks, Sonoma County. ....  
.....2b. *S. morrisonii* subsp. *morrisonii*
- D. Upper surfaces of rosette and lower cauline leaves heavily mottled with purple-brown, lower surface uniformly purplish; upper connate filaments uniformly yellow.



- E. Upper cauline leaves 2–4 times as long as wide. .... 2c. *S. morrisonii* subsp. *elatus*  
 E. Upper cauline leaves 1–2 times as long as wide. .... 2d. *S. morrisonii* subsp. *kruckebergii*

1. **STREPTANTHUS BRACHIATUS** F. W. Hoffm., Madroño 11:230. 1952.

Rosette leaves gray-green, mottled with purple-brown above, uniformly purple beneath. The original stem extending the second year and producing more or less brachiate branches bearing short-petiolate and sessile, undulate, auriculate, orbicular to orbiculate and oblong-spatulate, prominently veined leaves with entire or coarsely serrate margins or with the margins entire basally and serrate apically, passing into narrowly-lanceolate usually toothed bracts. Flowers in discrete racemes, bracteate or not. Calyces glabrous or sparsely pubescent and reticulate with fine lines, rose-purple with yellowish base or purple or yellow. Sepals broadly lanceolate. Upper connate filaments orange-colored with two longitudinal, purple lines. Chromosome number unknown.

- 1a. **STREPTANTHUS BRACHIATUS** F. W. Hoffm. subsp. **BRACHIATUS**. —  
 TYPE: USA, California, Sonoma–Lake county line, E of Pine Flat, exposed serpentine ridge near Contact Mine, 3000 ft, 5 Jun 1949, *Kruckeberg and Hoffman 1905* (holotypes, UC!).

Flowers glabrous; calyces rose-purple with yellowish bases; mature upper connate filaments orange with two longitudinal purple lines.

*Streptanthus brachiatus* subsp. *brachiatus* is known only from the immediate vicinity of Socrates Mine on the Sonoma–Lake county line (Fig. 1). According to H. K. Sharsmith (specimen annotation 8, Oct. 1952), the type locality is near the junction of Socrates Mine Rd, with Pine–Flat–Middletown Rd on ridge W of canyon of Big Sulphur Creek, Sonoma County. The Napa–Lake county line is on ridge east of canyon of Big Sulfur Creek.

*Additional collections.* USA, CA, Lake Co., near Contact Mine, E of Pine Flat, on the Sonoma–Lake county line, 3000 ft, *Kruckeberg and Hoffman 1905* (UC); same area, *Hoffman 3436* (UC); summit of ridge about 0.5 mi S of Mercuryville on rd to Big Geysers, *Hoffman 3379* (UC); Sonoma Co., near junction of Socrates Mine Rd with Pine–Flat–Middletown Rd, Mayacamas Mts., 3200 ft, *Sharsmith 4129* (UC).

- 1b. **Streptanthus brachiatus** F. W. Hoffman subsp. **hoffmanii** Dolan & LaPré, subsp. nov. —TYPE: USA, California, Lake County near Sonoma county line on Bear Ridge Rd ¼ mi S of three-way junction with Ridge Rd and Davies Rd, on serpentine outcrop near a geothermal expansion joint, 2 May 1985, *LaPré s.n.* (holotype, UC; isotypes, CAS, RSA, UC).



Herbae 10–30 cm altae probe basin ramossimae; calyces plerumque pubescentes, lutei vel atropurpurei.

Flowers glabrous to pubescent and variable within a population. Calyces purplish green to greenish yellow. Mature upper connate filaments yellowish with two dark-colored longitudinal lines.

This taxon occurs on isolated serpentine rock outcrops, occasionally scattered in adjacent chaparral, near the Lake–Sonoma county line (T10N R7W and R8W) primarily in geothermal development areas, from the junction of Ridge Road, Davies Road, and Bear Ridge Road off Socrates Mine Road, S to Buck Rock and SE to Mount St. Helena (Fig. 1). Populations are morphologically uniform within single outcrops but much local differentiation is present between outcrops, even those in close proximity. Calyx color varies most prominently (from purple to yellow) along with stature (from short to tall) along the line from the northwest to southeast. Populations in the southeast nearest the location of *S. morrisonii* subsp. *elatus* tend to converge on morphological characteristics of that taxon.

Species growing on the serpentine outcrops with *Streptanthus brachiatus* subsp. *hoffmanii* include the rare plants *Eriogonum nervulosum* and *Allium falcifolium*. Growing on the margins of the outcrops in the more weathered serpentine are *Pinus sabiniana*, *Arctostaphylos viscida*, *Cupressus sargentii*, *Quercus durata*, *Solanum parishii*, *Fremontodendron californicum* subsp. *napense*, and *Ceanothus jepsonii*.

This taxon is named in honor of Freed Hoffman, an amateur botanist, of Guerneville, CA, who specialized in serpentine flora. He was the first to collect *Streptanthus* in “The Geysers” region.

## 2. *STREPTANTHUS MORRISONII* F. W. Hoffm., Madroño 11:225. 1952.

Rosette leaves uniformly gray-green above and beneath, or the lower surface somewhat purple-tinged, or the upper surface heavily mottled with purplish or brownish blotches and the lower surface purple. The stem, in the second year, extended and producing auriculate-spatulate to auriculate-ovate, sessile, clasping, entire or few-toothed leaves, these passing into auriculate-lanceolate acute, sessile leaves and awl-shaped bracts. Flowers scattered along the flowering stems or concentrated towards the tips of branches. Calyces densely pubescent, with a few scattered hairs, or entirely glabrous, yellow to purple. Sepals ovate-lanceolate. Upper connate filaments uniformly yellow or orange with two longitudinal purple lines when the calyx is purple. Chromosome number unknown.

### 2a. *STREPTANTHUS MORRISONII* F. W. Hoffm. subsp. *HIRTIFLORUS* F. W. Hoffm., Madroño 11:228. 1952.—TYPE: USA, California, Sonoma County, on bluffs and cliff talus, serpentine soil, above



Dorr's Cabin, headwaters of East Austin Creek, 17 Jun 1948, *Hoffman 2344* (holotype, UC!).

Flowering stems strict or much branched and diffuse, up to 80 cm tall. Juvenile leaves heavily mottled with purple-brown above, uniformly purple beneath; upper stem leaves auriculate-spatulate to auriculate-ovate, sessile, clasping, entire or few toothed. Flowers abundant, scattered along the flowering branches. Calyces red-purple, abundantly clothed in long hairs (2 mm long) which gives the plant a grayish appearance. Petals dull white with purplish veins. Upper connate filaments orange, with two longitudinal, purple lines.

*Streptanthus morrisonii* subsp. *hirtiflorus* grows on serpentine bluffs and talus slopes with western exposure. This rare serpentine endemic occupies an area of not over 100 m<sup>2</sup> on west-facing serpentine bluffs and slopes at the headwaters of East Austin Creek, a short distance above Dorr's Cabin, Sonoma Co., California (Fig. 1). It has not been collected elsewhere.

- 2b. *STREPTANTHUS MORRISONII* F. W. Hoffm. subsp. *MORRISONII*. — TYPE: USA, California, Sonoma Co., serpentine outcrop, head of Big Austin Creek at Layton Mine, 26 Sep 1946, *Hoffman 1020* (holotype, UC!).

Flowering stems strict, 20–60 cm tall. Juvenile and adult leaves gray-green on both surfaces, or slightly purplish beneath, without maculation. Upper stem leaves similar to those of subsp. *hirtiflorus*. Flowers discretely produced toward the tips of the ascending or divergent branches. Calyces greenish yellow becoming golden yellow with age, glabrous or with a few scattered hairs. Petals creamy white to light salmon with brownish or orange-colored veins. Upper connate filaments uniformly orange.

This taxon occurs on serpentine outcrops in “The Cedars” area of northern Sonoma County, along the drainage of Big Austin Creek and its tributaries (Fig. 1).

*Additional collections.* USA, CA, Sonoma Co., headwaters of Big Austin Cr. at Layton Chromite Mine, *Hoffman 1020* (UC); Layton Mine, Austin Cr., *Hoffman 1027* (UC); near headwaters of Devil Cr., The Island: tributary of upper East Austin Cr., *Hoffman 2995* (UC); trail from Gray Cr. to The Island, headwaters of East Austin Cr., *Hoffman 3360* (UC); The Cedars, headwaters of East Austin Cr., 700–2000 ft, *Raiche 30581* (JEPS).

- 2c. *STREPTANTHUS MORRISONII* F. W. Hoffm. subsp. *ELATUS* F. W. Hoffm., Madroño 11:228. 1952. — TYPE: USA, California, Napa-Lake county line, ¼ mi W of White's Point, Table Mountain Rd, ca. 5 mi E of Mountain Mill House, 3 May 1947, *Kruckeberg 1438* (UC!).



Flowering stems strict, remotely branched, 35–105 cm tall. Juvenile leaves with upper surface mottled with purplish brown and lower surface uniformly purple, blades long-petioled, obovate or flabelliform, prominently veined, with margins entire basally and coarsely dentate distally. Upper stem leaves oblong-spatulate, cymbiform, clasping. Flowers produced toward the tips of ascending branches. Calyces greenish, turning golden yellow with age, glabrous or sparsely pubescent. Petals white, turning yellowish with age. Upper connate filaments uniformly greenish yellow.

Known only from several closely spaced serpentine outcrops near Three Peaks and White's Point on the Lake–Napa county line (Fig. 1).

*Additional collections.* USA, CA, southern Lake Co., along ridge from White Pt, near Napa–Lake county line, 2.7 mi E of Mt. Mill House, 2500 ft, *Hoffman 2906* (UC); *Hoffman 2872* (UC); rosettes grown from seed collected at White Pt, *Hoffman s.n.* (UC); Hoffman Cr., about 1 mi E of Mirabel Park, *Raven 010745* (UC).

2d. *Streptanthus morrisonii* F. W. Hoffm. subsp. *kruckebergii* Dolan & LaPré, subsp. nov.—TYPE: USA, California, Lake Co., Dunnigan Hill in Knoxville Recreation Area (T11N R5W, sect. 11), on serpentine outcrop, 8 Jun 1985, *LaPré s.n.* (holotype, UC; isotypes, CAS, RSA, UC).

Herbae 30–100 cm altae, remote ramosae, folia rosularia maculata purpureobrunneis in superioribus paginis, uniformiter purpurea in paginis inferis; folia caulina superiora 1–2plo longiora quam latiora; calyces glabrae vel leviter pubescentes, viridiflavae; superiora filamenta connata uniformiter lutea.

Flowering stems remotely branched, 20–115 cm tall. Juvenile leaves green with punctations above, uniformly purple beneath. Upper stem leaves oblong, spatulate, cymbiform, clasping, often deciduous before flowering. Flowers produced toward the tips of ascending branches. Calyces yellowish green, turning bright yellow with age. Petals creamy white. Upper connate filaments uniformly greenish yellow.

This new subspecies is a morphologically uniform taxon. The plant occurs on scattered serpentine outcrops near the Lake–Napa county line, primarily in the Knoxville Recreation Area (T11N R4W), Dunnigan Hill region, and associated watersheds (Fig. 1).

Species associated with *Streptanthus morrisonii* subsp. *kruckebergii* include *Eriogonum nervulosum*, *Allium falcifolium*, *Streptanthus breweri*, and *S. hesperidis*. *Pinus sabiniana*, *Arctostaphylos viscida*, *Cupressus sargentii*, *Quercus durata*, and *Ceanothus jepsonii* grow in the adjacent chaparral.

This taxon is named in honor of Dr. Arthur R. Kruckeberg, leading expert on the serpentine flora of the western United States.



## ACKNOWLEDGMENTS

This work was supported by Contract No. YA551-CT4-340080 between the U.S. Department of the Interior, Bureau of Land Management and Tierra Madre Consultants of Riverside, CA. Developers and utilities operating at the BLM's Known Geothermal Resource Area contributed funds to the project. Arthur Kruckeberg, Jim Bartel, and John Willowby provided helpful comments on the manuscript. Latin diagnoses were provided by Bert Steiner, Butler University. Holcomb Research Institute, Butler University, provided technical support.

## LITERATURE CITED

- HOFFMAN, F. W. 1952. Studies in *Streptanthus*. A new *Streptanthus* complex in California. *Madroño* 11:221–223.
- KRUCKEBERG, A. R. 1956. Variability in fertility of hybrids between isolated populations of the serpentine species, *Streptanthus glandulosus* Hook. *Evolution* 11: 185–211.
- . 1958. The taxonomy of the species complex, *Streptanthus glandulosus* Hook. *Madroño* 14:217–227.
- . 1984a. California's serpentines: flora, vegetation, geology, soils, and management problems. *Univ. Calif. Publ. Bot.* 78:1–180.
- . 1984b. California's serpentine. *Fremontia* 11:11–17.
- and J. L. MORRISON. 1983. New *Streptanthus* taxa (Cruciferae) from California. *Madroño* 30:230–244.
- MORRISON, J. L. 1941. A monograph of the section *Euclisia* Nutt., of *Streptanthus*. Ph.D. dissertation. Univ. of California, Berkeley.

(Received 29 Mar 1988; revision accepted 22 Nov 1988.)

## ANNOUNCEMENT

## FIFTH ANNUAL SOUTHWESTERN BOTANICAL SYSTEMATICS SYMPOSIUM

## “Endemism”

For information write to: Rancho Santa Ana Botanic Garden, Botanical Systematics and Evolution Symposium, 1500 N. College Ave., Claremont, CA 91711; phone (714) 625-8767. Date: 19–20 May 1989.



# CHROMOSOME NUMBERS OF NORTH AMERICAN *LATHYRUS* (FABACEAE)

S. L. BROICH

Department of Crop Science, Oregon State University,  
Corvallis, OR 97331

## ABSTRACT

Chromosome counts are reported for 18 populations of eight perennial *Lathyrus* species endemic to North America. Included are first counts of  $2n=14$  for *L. holochlorus* (Piper) C. Hitchc., *L. delnorticus* C. Hitchc., *L. glandulosus* Broich, *L. jepsonii* E. Greene subsp. *jepsonii* and *L. vestitus* Nutt. in Torrey & A. Gray subsp. *vestitus*, and  $2n=28$  for *L. nevadensis* S. Watson subsp. *nevadensis*. Chromosome counts of  $2n=14$  for *L. jepsonii* subsp. *californicus* (S. Watson) C. Hitchc., *L. vestitus* subsp. *bolanderi* (S. Watson) C. Hitchc., *L. polyphyllus* Nutt. in Torrey & A. Gray and *L. sulphureus* Brewer ex A. Gray agree with those reported previously. Karyotypes of diploid species are symmetrical and similar to one another. Among the species studied here there does not appear to be the reduction in chromosome size and DNA amount reported in the literature for annual, autogamous Mediterranean *Lathyrus* species.

*Lathyrus* L. is a genus of approximately 150 species of herbaceous perennial and annual papilionoid legumes (Fabaceae: Faboideae: Viciaeae). The genus is distributed primarily in temperate Europe, Asia, North America, and South America, and in North Africa (Senn 1938; Kupicha 1981, 1983). There are about 26 species of *Lathyrus* endemic to North America (Hitchcock 1952; Welsh 1965; Barneby and Reveal 1971; Broich 1983, 1986, 1987; Nelson and Nelson 1983; Welsh et al. 1987); chromosome numbers have been reported for 15 of these species (Senn 1938; Hitchcock 1952; Ledingham 1957; Brunsberg 1965; Raven et al. 1965; Taylor and Mulligan 1968; Löve and Löve 1982; Ward 1983).

The purpose of this paper is to report new observations of chromosome number and morphology of species of *Lathyrus* endemic to North America and to place these observations within the context of the genus world-wide.

## MATERIALS AND METHODS

Seeds of native *Lathyrus* were collected in July of 1979, 1980, and 1981. In addition to the author's collections, seeds of *L. jepsonii* E. Greene subsp. *jepsonii* were obtained from W. Roderick (Tilden Park Botanical Garden, Berkeley, CA), of *L. vestitus* Nutt. in Torrey & A. Gray and *L. laetiflorus* E. Greene (= *L. vestitus* subsp. *vestitus* sensu Broich, 1987) were obtained from Mary Allcott (Santa Barbara Botanic Garden, Santa Barbara, CA) and of *L. vestitus* from Mon-



terey County, CA, were obtained from Dr. J. R. Griffin (Hastings Natural History Reservation, Carmel Valley, CA).

Seeds were scarified with a razor blade and stored in rolls of damp germination paper (Dillard Paper Co., Doraville, GA) in a refrigerator at ca. 5°C for 2 months. Five to six rolls were then placed vertically in a glass jar containing 100 ml of tap water, covered with a clear plastic bag and placed in a growth chamber on a cycle of 18 hours light at 22°C and 6 hours darkness at 18°C. After germination, seedlings were transplanted to the greenhouse into a soil mixture of equal parts of sand, peat, and soil.

The number and morphology of mitotic chromosomes were studied by examining root tip squashes. Root tips were pretreated with distilled water saturated with para-dichlorol-benzene at 10–15°C for 4 hours, fixed in 95% ethanol:glacial acetic acid (3:1; v:v), hydrolyzed in 1 N HCl for 20 minutes at 60°C, stained in Feulgen (Darlington and La Cour 1975) and stored in 70% ethanol in a refrigerator (ca. 5°C). Stained root tips were squashed in 45% acetic acid and examined and photographed on a Zeiss phase-contrast microscope; slides were not made permanent.

Voucher specimens, deposited at Oregon State University Herbarium (OSC), were made from two sources: specimens of plants taken from populations where seeds were later collected (field vouchers), and specimens of the plants from which root tips were taken (greenhouse vouchers). The species of *Lathyrus* studied here did not flower under greenhouse conditions, therefore the greenhouse voucher specimens are of vegetative stems only.

## RESULTS

Table 1 presents a summary of new chromosome counts for Pacific Coast *Lathyrus*. First counts of  $2n=14$  were determined for *L. glandulosus*, *L. holochlorus*, *L. delnorticus*, *L. jepsonii* subsp. *jepsonii* and *L. vestitus* subsp. *vestitus*, and a count of  $2n=28$  for *L. nevadensis* subsp. *nevadensis*. Additional counts of  $2n=14$  for *L. jepsonii* subsp. *californicus*, *L. polyphyllus*, *L. sulphureus*, *L. vestitus* subsp. *bolanderi* agree with the reports of Hitchcock (1952).

Karyotypes of all species examined are symmetrical and fall into classes 1A and 1B described by Stebbins (1971). Chromosome complements of these species are similar to one another; there is less than 25% difference in total haploid chromosome length among all diploid species examined. Chromosomes within a species are also similar to one another; the ratio of longest to shortest chromosome within a given species ranged from 1.4 to 1.7. The genome of each diploid species consists of 3–4 metacentric chromosomes decreasing in length from 7.1 to 5.5 micrometers and 4–3 submetacentric chromosomes also decreasing in length from ca. 7.0 to 5.0 micrometers.



TABLE 1. NEW CHROMOSOME COUNTS OF PACIFIC COAST SPECIES OF *LATHYRUS*. An asterisk indicates first count(s) for that taxon.

---

|  |
|--|
| * <i>L. delnorticus</i> C. Hitchc. $2n=14$ . CA, Del Norte Co., Panther Flat Campground, Six Rivers National Forest, T16N R3E sect. 22, <i>Broich</i> 642 (OSC); along French Hills Rd, 0.5 km S of jctn with Hwy 199, T17N R1E sects. 24–25, <i>Broich</i> 654 (OSC).   |
| * <i>L. holochlorus</i> (Piper) C. Hitchc. $2n=14$ . OR, Benton Co., along Oak Creek Rd ca. 0.4 km S of entrance to McDonald State Forest, T11S R5W sect. 19, <i>Broich</i> 1298 (OSC); Linn Co., along Hwy 99E opposite Linn-Benton Community College, T11S R4W sect. 36, <i>Broich</i> 630 (OSC).  |
| * <i>L. glandulosus</i> Broich. $2n=14$ . CA, Humboldt Co., 0.6 km E of the Freshwater-Kneeland Rd on rd to Maple Cr., <i>Broich</i> 772 (OSC); ca. 6.4 km S of the Kneeland School on rd to Bridgeville, <i>Broich</i> 777 (OSC).   |
| * <i>L. jepsonii</i> E. Greene subsp. <i>jepsonii</i> . $2n=14$ . CA, Contra Costa Co., Brown's Island near Pittsburg. Plants grown in greenhouse from seed provided by W. Roderick, Tilden Park Bot. Gard., Berkeley, CA, <i>Broich</i> 1278 (OSC).   |
| <i>L. jepsonii</i> E. Greene subsp. <i>californicus</i> (S. Watson) C. Hitchc. $2n=14$ . CA, Trinity Co., 1.3 km E of Dinsmore's on Hwy 36, T30N R5E sect. 3, <i>Broich</i> 1166 (OSC).  |
| * <i>L. nevadensis</i> subsp. <i>nevadensis</i> . $2n=28$ . OR, Benton Co., ca. 0.2 km S of entrance to McDonald State Forest, T121S R5W sect. 19, <i>Broich</i> 608 (OSC).  |
| <i>L. polyphyllus</i> Nutt. in Torrey & A. Gray. $2n=14$ . CA, Siskiyou Co., 3.9 km N of Happy Camp on rd to Takilma, Oregon, <i>Broich</i> 1182 (OSC). OR, Linn Co., along Peoria Rd, T12S R4W sect. 8, <i>Broich</i> 615 (OSC). Benton Co., McDonald State Forest, ca. 300 m N of the Oak Creek Entrance, T11S R5W sect. 19, <i>Broich</i> 1103 (OSC); along Peterson Rd, T12S R6W sect. 35, <i>Broich</i> 603 (OSC).  |
| <i>L. sulphureus</i> Brewer ex A. Gray. $2n=14$ . OR, Josephine Co., 0.8 km S of Waldo on FS rd 40S03, T40S R8W sect. 28, <i>Broich</i> 1131 (OSC).  |
| * <i>L. vestitus</i> Nutt. in Torrey & A. Gray subsp. <i>vestitus</i> . $2n=14$ . CA, Monterey Co., S slope of Junipero Serra Peak, Los Padres National Forest, T21S R5E sect. 4, plants grown in greenhouse from seed provided by J. R. Griffin, Hastings Natural History Reservation, Carmel Valley, <i>Broich</i> 1277 (OSC). Santa Barbara Co., plants grown in greenhouse from seed provided by Mary Allcott, Santa Barbara Botanic Garden, <i>Broich</i> 1267 (OSC). Ventura Co., ca. 64 km S of Ventucopa on Hwy 33, Los Padres National Forest, <i>Broich</i> 808 (OSC). |
| <i>L. vestitus</i> subsp. <i>bolanderi</i> (S. Watson) C. Hitchc. $2n=14$ . CA, Del Norte Co., Panther Flat Campground, Six Rivers National Forest, T17N R3E sect. 22, <i>Broich</i> 643 (OSC).  |

---

Chromosomes in the tetraploid *L. nevadensis* were also metacentric to submetacentric and of approximately the same length as those of diploid species.

On average, 5–10 good metaphase spreads were observed per root tip prepared, but in most cases only 1–2 photographs per plant were taken for measurement. Differences in degree of contraction were observed on slides and also among the photographs taken. Given the small sample size for each species and the karyotype similarity among species studied, interspecific differences could not be detected over the possible sources of error involved in karyotype measurements (Bentzer et al. 1971).



TABLE 2. A CATALOGUE OF CHROMOSOME COUNTS FOR SPECIES OF *LATHYRUS* ENDEMIC TO NORTH AMERICA. (\* indicates reported herein; see Table 1.)

| Species   | <i>n</i> | <i>2n</i> | Previous report(s)                              |
|---|----------|-----------|---|
| <i>L. biflorus</i> Nelson & Nelson                |          | unknown   | —   |
| <i>L. bijugatus</i> White                         |          | unknown   | —   |
| <i>L. brachycalyx</i> Rydb.                       |          |           |   |
| var. <i>brachycalyx</i>                           | —        | 14        | Hitchcock 1952                                  |
| var. <i>zionis</i> (C. Hitchc.) Welsh             | —        | 14        | Hitchcock 1952 [as <i>L. zionis</i> C. Hitchc.] |
| <i>L. delnorticus</i> C. Hitchc.                  | —        | 14*       | —   |
| <i>L. eucosmus</i> Butters & St. John             | —        | 14        | Hitchcock 1952                                  |
| <i>L. glandulosus</i> Broich                      | —        | 14*       | —   |
| <i>L. graminifolius</i> (S. Watson) T. White      | 7        | —         | Hitchcock 1952; Ward 1983                       |
| <i>L. hitchcockianus</i> Barneby & Reveal         |          | unknown   | —   |
| <i>L. holochlorus</i> (Piper) C. Hitchc.          | —        | 14*       | —   |
| <i>L. jepsonii</i> E. Greene                      |          |           |   |
| subsp. <i>jepsonii</i>                            | —        | 14*       | —   |
| subsp. <i>californicus</i> (S. Watson) C. Hitchc. | 7        | 14*       | Hitchcock 1952                                  |
| <i>L. lanszwertii</i> Kellogg                     |          |           |   |
| subsp. <i>lanszwertii</i>                         | 14       | 14, 28    | Hitchcock 1952                                  |
| subsp. <i>aridus</i> (Piper) R. Bradshaw          | 7        | 14        | Hitchcock 1952                                  |
| var. <i>arizonicus</i> (Britton) Welsh            | 14       | 28        | Hitchcock 1952 [as <i>L. arizonicus</i> ]       |
| var. <i>laetivirens</i> (E. Greene) Welsh         |          | unknown   | —   |
| <i>L. littoralis</i> (Nutt.) Endl.                | —        | 28        | Taylor and Mulligan 1968                        |
| <i>L. longipes</i> T. White                       |          | unknown   | —   |
| <i>L. nevadensis</i> S. Watson                    |          |           |   |
| subsp. <i>nevadensis</i>                          | —        | 28*       | —   |
| subsp. <i>cusickii</i> (S. Watson) C. Hitchc.     |          | unknown   | —   |
| subsp. <i>lanceolatus</i> (Howell) C. Hitchc.     | 14       | 28        | Hitchcock 1952                                  |



TABLE 2. CONTINUED.

| Species   | <i>n</i> | <i>2n</i> | Previous report(s)  |
|---|----------|-----------|---|
| <i>L. ochroleucus</i> Hook.                     | —        | 14        | Senn 1938; Ledingham 1957; Löve and Löve 1982   |
| <i>L. parviflorus</i> S. Watson                 | —        | unknown   | —   |
| <i>L. pauciflorus</i> Fern.                     |          |           |   |
| subsp. <i>pauciflorus</i>                       |          | unknown   | —   |
| subsp. <i>brownii</i> (Eastw.) Piper            |          | unknown   | —   |
| <i>L. polymorphus</i> Nutt.                     |          | unknown   | —   |
| <i>L. polyphyllus</i> Nutt. in Torrey & A. Gray | —        | 14*       | Hitchcock 1952  |
| <i>L. rigidus</i> T. White                      | —        | 14        | Hitchcock 1952  |
| <i>L. splendens</i> Kellogg                     | 7        | 14        | Hitchcock 1952  |
| <i>L. sulphureus</i> Brewer ex A. Gray          | 7        | 14*       | Hitchcock 1952  |
| <i>L. torreyi</i> A. Gray                       | 7        | —         | Hitchcock 1952  |
| <i>L. tracyi</i> R. Bradshaw                    | 7        | —         | Hitchcock 1952  |
| <i>L. venosus</i> Muhl. ex Willd.               | 14       | 28        | Senn 1938; Ledingham 1957; Löve and Löve 1982   |
| <i>L. vestitus</i> Nutt. in Torrey & A. Gray    |          |           |   |
| subsp. <i>vestitus</i>                          | —        | 14*       | —   |
| subsp. <i>laetiflorus</i> (E. Greene) Broich    | —        | 14        | Brunsberg 1965 [as <i>L. laetiflorus</i> E. Greene]                                     |
| subsp. <i>alefeldii</i> (T. White) Broich       | 7        | —         | Hitchcock 1952 [as <i>L. laetiflorus</i> subsp. <i>alefeldii</i> (T. White) C. Hitchc.] |
| subsp. <i>bolanderi</i> (S. Watson) C. Hitchc.  | 7        | 14*       | Hitchcock 1952  |
| subsp. <i>laevicarpus</i> Broich                | 7        | —         | Raven et al. 1965 [as <i>L. laetiflorus</i> E. Greene]                                  |



## DISCUSSION

*Lathyrus* is widespread in temperate regions of both the Old and New World. Bassler (1973) and Raven and Axelrod (1978) have suggested that the genus originated in the Arcto-Tertiary geoflora of the Eocene. *Lathyrus* now consists of approximately 75% perennials and 25% annuals organized into 13 sections (Kupicha 1983). Six sections consist exclusively of perennials, six sections of annuals and one section includes both perennials and annuals. All species endemic to North America are perennials and included in the section *Orobis* (L.) Godron in Gren. & Godron, which contains about one-third of all *Lathyrus* species.

*Lathyrus* L. is predominantly diploid at  $2n=2x=14$ . Kupicha (1977), in a summary table of counts for 56 species, reports five species which deviate from this number; Fedorov (1969) listed five polyploid species and two aneuploids (one  $2n=12$ ; one  $2n=16$ ) of 61 species reported. The Fedorov list, however, does not include counts reported by Hitchcock (1952). When information from Hitchcock (1952) and more recent compilations (Moore 1973; Goldblatt 1981, 1984, 1985) are taken into account, a total of seven polyploid taxa have been reported in *Lathyrus*. All polyploid taxa are perennial and belong to the section *Orobis* except *L. patensis* L. ( $2n=14, 28, 42$ ) which has been placed in sect. *Pratensis* Bassler (Kupicha 1983).

With the new determinations reported here, a sample of chromosome numbers is now known for 18 of the 26 *Lathyrus* species endemic to North America (Table 2). North America appears to be a center for polyploidy in *Lathyrus*: four of the seven known polyploid species (*L. venosus* Muhl.,  $2n=28$ ; *L. nevadensis* S. Watson,  $2n=28$ ; *L. littoralis* (Nutt. ex Torrey & A. Gray) Endl.,  $2n=28$ ; *L. lanzwertii* Kellogg,  $2n=14, 28$ ) are endemic to the continent; two of the remaining three (*L. japonicus* Willd.,  $2n=14, 28$ ; *L. palustris* L.,  $2n=42$ ) have circumboreal distributions and are native to North America. The complete extent and significance of polyploidy in North American *Lathyrus* have yet to be studied in detail.

Variation in the amount of genome DNA among *Lathyrus* species has also been studied (Rees and Hazarika 1969; Narayan 1982). Annual, autogamous species, which have evolved in the Mediterranean region, exhibit a threefold decrease in chromosome size correlated to a fourfold decrease in the amount of nuclear DNA per diploid nucleus. In contrast, all western North American species of *Lathyrus* are perennial. Of those occurring along the Pacific Coast, *L. vestitus* subsp. *bolanderi*, *L. holochlorus*, and *L. polyphyllus* have been found to be self-incompatible (Broich 1983). *L. vestitus* is reported as having the greatest amount of nuclear DNA of the 21 species studied by Narayan (1982), and if chromosome size can be



taken to indicate, approximately, nuclear DNA amounts within a genome, the other species studied here have similar high amounts of DNA in comparison to the annual species of the Mediterranean Region. New chromosome observations reported here, therefore, corroborate the correlation between reduced DNA amounts and the evolution of an annual habit reported for *Lathyrus* (Rees and Hazarika 1969) and for higher plants in general (Price 1976).

#### ACKNOWLEDGMENTS

I wish to thank Kenton Chambers for his support of this project and Mary Alcott, W. Roderick, and especially James R. Griffin for graciously responding to requests for seed of California *Lathyrus* species. Funds for this project were provided by the Oregon State University Herbarium and by National Science Foundation grant DEB-7911543.

#### LITERATURE CITED

- BARNEBY, R. C. and J. L. REVEAL. 1971. A new species of *Lathyrus* (Fabaceae) from the Death Valley region of California and Nevada. *Aliso* 7:361–364.
- BASSLER, M. 1973. Revision der eurasiatischen Arten von *Lathyrus* L. sect. *Orobis* (L.) Gren. & Godron. *Feddes Repert.* 84:329–347.
- BENTZER, B., R. V. BOTHMAR, L. ENGSTRAND, M. GUSTAFSSON, and S. SNOGERUP. 1971. Some sources of error in the determination of arm ratios of chromosomes. *Bot. Not.* 124:65–74.
- BROICH, S. L. 1983. A systematic study of *Lathyrus vestitus* Nutt. ex T. & G. (Fabaceae) and allied species of the Pacific Coast. Ph.D. thesis. Oregon State University, Corvallis, OR.
- . 1986. A new species of *Lathyrus* (Fabaceae) from northwestern California. *Madroño* 33:136–143.
- . 1987. Revision of the *Lathyrus vestitus-laetiflorus* complex (Fabaceae). *Syst. Bot.* 12:139–153.
- BRUNSBURG, K. 1965. The usefulness of thin-layer chromatographic analysis of phenolic compounds in European *Lathyrus* L. *Bot. Not.* 118:377–402.
- DARLINGTON, C. D. and L. F. LACOUR. 1975. The handling of chromosomes, 6th ed. John Wiley and Sons, New York.
- FEDOROV, A. A. 1969. Chromosome numbers of flowering plants. Izdatel'stvo Nauk, Leningrad, U.S.S.R.
- GOLDBLATT, P. 1981. Index to plant chromosome numbers, 1975–1978. Missouri Botanical Garden, St. Louis, MO.
- . 1984. Index to plant chromosome numbers, 1979–1981. Missouri Botanical Garden, St. Louis, MO.
- . 1985. Index to plant chromosome numbers, 1982–1983. Missouri Botanical Garden, St. Louis, MO.
- HITCHCOCK, C. L. 1952. A revision of the North American species of *Lathyrus*. Univ. Wash. Publ. Biol. 15:1–104.
- KUPICHA, F. K. 1981. Tribe 21. Viciae (Adans.) DC. Pp. 377–381 in R. M. Polhill and P. H. Raven (eds.), *Advances in legume systematics*. Royal Botanic Gardens, Kew, U.K.
- . 1983. The infrageneric structure of *Lathyrus*. *Notes Roy. Bot. Gard. Edinburgh* 41(2):209–244.
- LEDINGHAM, G. F. 1957. Chromosome numbers of some Saskatchewan Leguminosae with particular reference to *Astragalus* and *Oxytropis*. *Can. J. Bot.* 35:657–666.



- LÖVE, A. and D. LÖVE. 1982. IOPB chromosome number report LXXV. *Taxon* 31: 344–360.
- MOORE, R. J. 1973. Index to Plant chromosome numbers, 1967–1971. *Regnum Vegetabile* No. 90.
- . 1972. Index to Plant chromosome numbers, 1972. *Regnum Vegetabile* No. 91.
- NARAYAN, R. K. J. 1982. Discontinuous DNA variation in the evolution of plant species: the genus *Lathyrus*. *Evolution* 36:877–891.
- NELSON, T. W. and J. P. NELSON. 1983. Two new species of Leguminosae from serpentine of Humboldt County, California. *Brittonia* 35:180–183.
- PRICE, H. J. 1976. Evolution of DNA content in higher plants. *Bot. Rev.* 42: 27–52.
- RAVEN, P. H. and D. I. AXELROD. 1978. Origin and relationships of the California flora. *Univ. Calif. Publ. Bot.* 72:1–134.
- , D. W. KYHOS, and A. J. HILL. 1965. Chromosome numbers of spermatophytes, mostly Californian. *Aliso* 6:105–113.
- REES, H. and M. H. HAZARIKA. 1969. Chromosome evolution in *Lathyrus*. *Chromosomes Today* 2:158–165.
- SENN, H. A. 1938. Experimental data for a revision of the genus *Lathyrus*. *Amer. J. Bot.* 25:67–78.
- STEBBINS, G. L. 1971. Chromosome evolution in higher plants. Addison-Wesley, Reading, MA.
- TAYLOR, R. L. and G. A. MULLIGAN. 1968. The flora of the Queen Charlotte Islands II: cytological aspects of the vascular plants. Queen's Printer, Ottawa, Canada.
- WARD, D. E. 1983. Chromosome counts from New Mexico and southern Colorado. *Phytologia* 54:302–309.
- WELSH, S. L. 1965. Legumes of Utah. III. *Lathyrus* L. *Proc. Utah Acad. Sci.* 42: 214–221.
- , N. D. ATWOOD, L. C. HIGGINS, and S. GOODRICH. 1987. A Utah flora. Great Basin Naturalist Mem. 9, Brigham Young Univ., Provo, UT.

(Received 13 Jul 1988; revision accepted 7 Dec 1988.)



## NOTES

*GENTIANA SETIGERA* IS THE CORRECT NAME FOR *G. BISETAEA* (GENTIANACEAE).—*Gentiana bisetaea* Howell (Fl. N.W. Amer., 445, 1901) is a localized but fairly well understood species found in *Darlingtonia* bogs and seeps on serpentine hillsides in southwestern Oregon. The type locality given by Howell is “. . . eastern base of the Coast Mountains near Waldo, Oregon,” the town of Waldo being a once-thriving gold-mining community in the southern part of the upper Illinois River Valley in Josephine County. Today the species is known from numerous bogs between Eight Dollar Mountain, 19 km N of Waldo, S to Gasquet Mountain, Del Norte Co., CA, and at scattered sites westward in the rugged Siskiyou Mountains to Curry Co., OR (files of Oregon Natural Heritage Data Base, Portland, and Siskiyou National Forest, Grants Pass). In 1941 M. E. Peck (Man. Higher Pl. Oregon, 1st ed., 558) synonymized *G. bisetaea* with *G. setigera* A. Gray, a California taxon, but in the second edition of his book (607, 1961) and in L. R. Abrams’ “Illustrated Flora of the Pacific States” (3:358, 1951) *G. bisetaea* is treated as a distinct species. Because of its restricted range and specialized habitat, this gentian has been considered for possible listing as an endangered or threatened species (R. J. Meinke, “Threatened and Endangered Plants of Oregon: An Illustrated Guide,” U.S. Fish & Wildlife Service, 160, 1982).

The name *Gentiana setigera* A. Gray, in the usage of California botanists, has for over 60 years been applied to quite a different species from *G. bisetaea* (see descriptions and illustrations in Jepson, Fl. Calif. 3:91, 1939; Abrams, loc. cit.; Munz, A California Fl., 442, 1959). However, in an unpublished manuscript, C. T. Mason, Jr. (1981) stated that *G. setigera* is actually the earliest name for *G. bisetaea*, and that a new name is needed for the species that has been confused with *G. setigera* in the various floras. In order to determine the correct application for the name *G. setigera*, we have reviewed pertinent literature and reexamined the holotype specimen (Bolander, No. 840 of the Kellogg and Harford distribution, GH!). Additionally, one of us (J.G.) visited the type locality (Red Mountain, Mendocino Co., CA) in company with Joann Holm, U.S. Bureau of Land Management, and collected a suite of specimens of the one *Gentiana* species found there (*Greenleaf* 1458, 4 Oct 1983, 2 sheets JEPS, 4 sheets OSC). We have seen only one further collection from the type locality (*C. P. Bonsall s.n.*, 1933, JEPS!). As discussed below, the critical morphological features of the holotype as well as the recently collected topotypes strongly support Mason’s contention that *G. setigera* and *G. bisetaea* are synonymous.

The misunderstanding by Jepson, Abrams, and others about the identity of *G. setigera* may have been due both to ambiguities in Gray’s published description of the taxon and to these authors’ unfamiliarity with the Oregon populations, named *G. bisetaea* by Howell. Gray’s original description in Latin (Proc. Amer. Acad. 11: 84, 1876) and his later ones in English (Synoptical Fl. No. Amer. 2[1]:121, 1878; Bot. Calif. 1:482, 1880) fit the Bolander type-specimen very well, except that they do not emphasize enough the strikingly decumbent stems and overlook entirely the tuft of basal rosette leaves. One oblanceolate, acute rosette leaf is nearly hidden by a stem but is at least 5 cm long; another one, clearly exposed, is 4 cm long and 1 cm wide. At least four more rosette leaves are present and are 2–3 cm long. A basal tuft of leaves from the caudex is very characteristic of *G. bisetaea* but is poorly developed in the plants previously assigned to *G. setigera*. The flowering stems of the Bolander type resemble *G. bisetaea* in having closely spaced and fairly numerous lower leaf-pairs, mostly with well-developed blades, with longer internodes distally and narrower-bladed leaves at the upper nodes. The lower cauline leaves have unusually broad blades (examples of length: width in cm are 2.0:1.5, 2.4:1.7, 2.3:1.6, 2.1:1.6), differing in this respect from the majority of *G. bisetaea* plants in Oregon. However,



the 1983 population sample from Red Mountain, while notably broad-leaved, includes some individuals that are indistinguishable from typical *G. bisetata* both in habit and in leaf shape.

Gray described the upper two pairs of stem leaves of *G. setigera* as forming an involucre to the solitary terminal flower. The 1983 collections from Red Mountain show this to be a variable trait, however; most plants have only the uppermost leaf-pair subtending the flower—as is typical of *G. bisetata*. The variation in form of the appendages of the corolla sinuses is identical in *G. bisetata* and *G. setigera*, both as described by Gray from the Bolander type and as noted in the 1983 samples from Red Mountain. We observed that the flowers of many plants on Red Mountain were paler blue than those in the Illinois Valley area, especially on the outer surface of the corolla.

Those gentians from northwestern California and adjacent Oregon, to which the name *G. setigera* has been misapplied, differ from the plants described above in having strictly erect or ascending stems, a poorly developed basal rosette, broad cauline leaves nearly alike (except the lowest 2–3 pairs) and at equally spaced nodes up the stem, often several flowers at the apex, and corolla sinuses often with more numerous capillary appendages. Further study may show these plants to be distinct from the closely related *G. calycosa* Grisebach and worthy of species status.

The Red Mountain population of *G. setigera* (= *G. bisetata*) is about 225 km south of the nearest sites in Del Norte Co. and southwestern Oregon. It occurs in a wet meadow on a serpentine ridge at ca. 1065 m elevation. As presently understood, this species is rare in California, and due to the misuse of its name for a different taxon, its listing in the “Inventory of Rare and Endangered Vascular Plants of California” (Smith and Berg, CNPS Spec. Publ. No. 1, 4th ed., 58, 1988) should be reevaluated. In Oregon *G. setigera* is threatened by prospective nickel mining, although due to economic considerations it seems unlikely that extraction and smelting of nickel ore will occur in the near future. The nomenclatural change from *G. bisetata* to *G. setigera* has little effect on the biological status of the species, as only a single widely disjunct population in California is being added to its previously known occurrences.

We thank James Hickman for his help and encouragement with this study. Travel funds were provided by the Oregon State University Herbarium. — KENTON L. CHAMBERS and JACQUELINE GREENLEAF, Department of Botany and Plant Pathology, Oregon State University, Corvallis, OR 97331. (Received 23 Nov 1987; revision accepted 15 Oct 1988.)

---

INFRA-SPECIFIC NAME CHANGES IN *LIMNANTHES* (LIMNANTHACEAE). — In anticipation of a new edition of Jepson’s “Manual of the Flowering Plants of California”, it is necessary to make certain nomenclatural changes to provide uniformity throughout the genus *Limnanthes*.

The International Code (Voss, 1983, Regnum Veg. 111) provides no definitions for the taxa, subspecies and variety, and accordingly no distinction is made other than sequence if both are used.

At the time of my *Limnanthes* monograph (Mason, 1952, Univ. Calif. Publ. Bot. 25:455–512) I chose variety as the rank for the infraspecific taxa. In 1973 Arroyo (Brittonia 25:177–191) described several new taxa which she called subspecies. These appear to be taxonomically the same as my varieties. The following changes are made to elevate the several varieties to subspecies, and thereby standardize the taxonomy.

***Limnanthes douglasii* R. Br. subsp. *sulphurea* (C. Mason) C. Mason, stat. nov.** — *Limnanthes douglasii* var. *sulphurea* C. Mason, Univ. Calif. Publ. Bot. 25:477. 1952.

***Limnanthes douglasii* R. Br. subsp. *nivea* (C. Mason) C. Mason, stat. nov.** — *Limnanthes douglasii* var. *nivea* C. Mason, Univ. Calif. Publ. Bot. 25:477. 1952.

***Limnanthes douglasii* R. Br. subsp. *rosea* (Benth.) C. Mason, stat. nov.** — *Limnanthes rosea* Benth., Pl. Hartw. 302. 1848.



***Limnanthes gracilis*** Howell subsp. *parishii* (Jepson) C. Mason, stat. nov.—*Limnanthes versicolor* (E. Greene) Rydb. var. *parishii* Jepson, Fl. Calif. 2:411. 1936.  
***Limnanthes alba*** Hartweg in Benth. subsp. ***versicolor*** (E. Greene) C. Mason, stat. nov.—*Floerkea versicolor* E. Greene, Erythea 3:62. 1895.

—CHARLES T. MASON, JR., University of Arizona Herbarium, Tucson, AZ 85721.  
(Received 21 Jul 1988; revision accepted 2 Dec 1988.)

---

REAPPRAISAL OF THE RANGE OF *PHACELIA VALLICOLA* (HYDROPHYLLACEAE).—Discovery of disjunct populations of *Phacelia vallicola* Congdon ex Brand (Hydrophyllaceae) in Nevada and Sierra cos., California, inspired a search of major California herbaria for more information on the plant's distribution and habitat requirements. Until now *P. vallicola* was known from the W side of the Sierra Nevada in Mariposa, Tuolumne, Placer, and El Dorado cos. (Lee, Noteworthy collections, Madroño 30: 129, 1983). The collections listed below from Butte, Madera, Nevada, Shasta, and Sierra cos. extend the known range more than 200 km (Fig. 1).

*Specimens examined.* CA, Butte Co., overlook on the Skyway 4.2 km S of Neal Rd, T22N R3E NW¼ of SE¼ sect. 30, on the side of Tuscan outcrops on the rim of Little Butte Cr. Canyon, foothill woodland-chaparral ecotone, 335 m, 16 Apr 1986, *Oswald 1069* (CHSC); Hwy 70 at SE entrance of Grizzly Dome Tunnel, along base of granite cliff in decomposed granite, 17 Apr 1976, *Lickey 75* (CHSC); E of Feather Falls ca. 13 km, on dry bare lava cap, yellow pine f., 1000 m, 4 Jun 1982, *Ahart 3534* (CHSC); Lumpkin Ridge, E of village of Feather Falls, T21N R7E sect. 36, in open on Lovejoy basalt, yellow pine f., 20 May 1981, *Schlising 4060* (CHSC); ca. 12.9 km NE of Feather Falls, on dry bare broken black lava, yellow pine f., 1280 m, 12 May 1987, *Ahart 5627* (CHSC). Madera Co., Canyon of Nelder Cr. ca. 16 km N of Oakhurst, slopes E of creek, T6S R21E SE¼ of SE¼ sect. 30, small domal granite outcrops in brushy yellow pine f., 9 May 1984, *Jokerst 1999* (CHSC). Nevada Co., NW of Emigrant Gap 8 km, 0.8 km N of South Yuba River, T17N R11E SW¼ sect. 2, foothill woodland, on metamorphic parent material, 1 May 1985, *Bowcutt 499* (UC); W of Lake Spaulding dam 0.8 km, along Bowman Lake Rd 2.9 km from Hwy 80, 12.8 km SE of Washington, 0.2 km W of South Yuba River, T17N R11E SW¼ sect. 2, foothill woodland, on metamorphic rock outcrop and talus 1418 m, 1 May 1985, *Bowcutt 501* (UC). Placer Co., N of Long Canyon Cr., E of Blacksmith Flat, T13N R13E NW¼ of SW¼ sect. 7, on rock talus and bedrock outcrops in openings in S facing slopes, mixed coniferous f. and chaparral, 1128 m, 19 Jun 1984, *Jokerst 2057* (CHSC). Shasta Co., 4.8 km E of Hwy 5, along Gilman Rd near Shasta Lake, 11 May 1983, *Lennon s.n.* (DAV, JEPS). Sierra Co., Lavezzola Creek Canyon, 12 km NE of Downieville, along U.S. Forest Service trail, T21N R11E SW¼ of NW¼ sect. 33, 1390 m, 5 Aug 1985, *Bowcutt 649* (UC); N of Pacific Mine ca. 0.4 km, ca. 8 km E of LaPorte, on dry bare rocky soil in yellow pine f., 28 Jul 1982, *Ahart 3690* (CHSC); on dry rocky ridge above Foote Rd, ca. 8 km S of Alleghany, yellow pine f., 1219 m, 4 Jun 1978, *Ahart 1770* (CHSC).

*Habitats.* The following habitat description is based on herbarium label data and field observations over three years. The herbarium data presented above do not include the forty specimens collected in Mariposa and Tuolumne cos. that are housed at CAS, CHSC, HSU, JEPS, and UC. However, the range of habitats and elevations for these counties is represented in the description. *Phacelia vallicola* is found on granitic, metamorphic, and volcanic rock outcrops and talus slopes in foothill woodland, yellow pine forest, mixed coniferous forest, and chaparral communities. According to Munz (UC Press, 1973), *Phacelia vallicola* also occurs in red fir forest; however, I have not seen any specimens collected from this plant community. The species' known elevational range is from 335 to 2134 m. The plant is often common but scattered where it occurs. Most known populations are on U.S. Forest Service lands. Possible threats include hydroprojects and mining. Indirect impacts could result



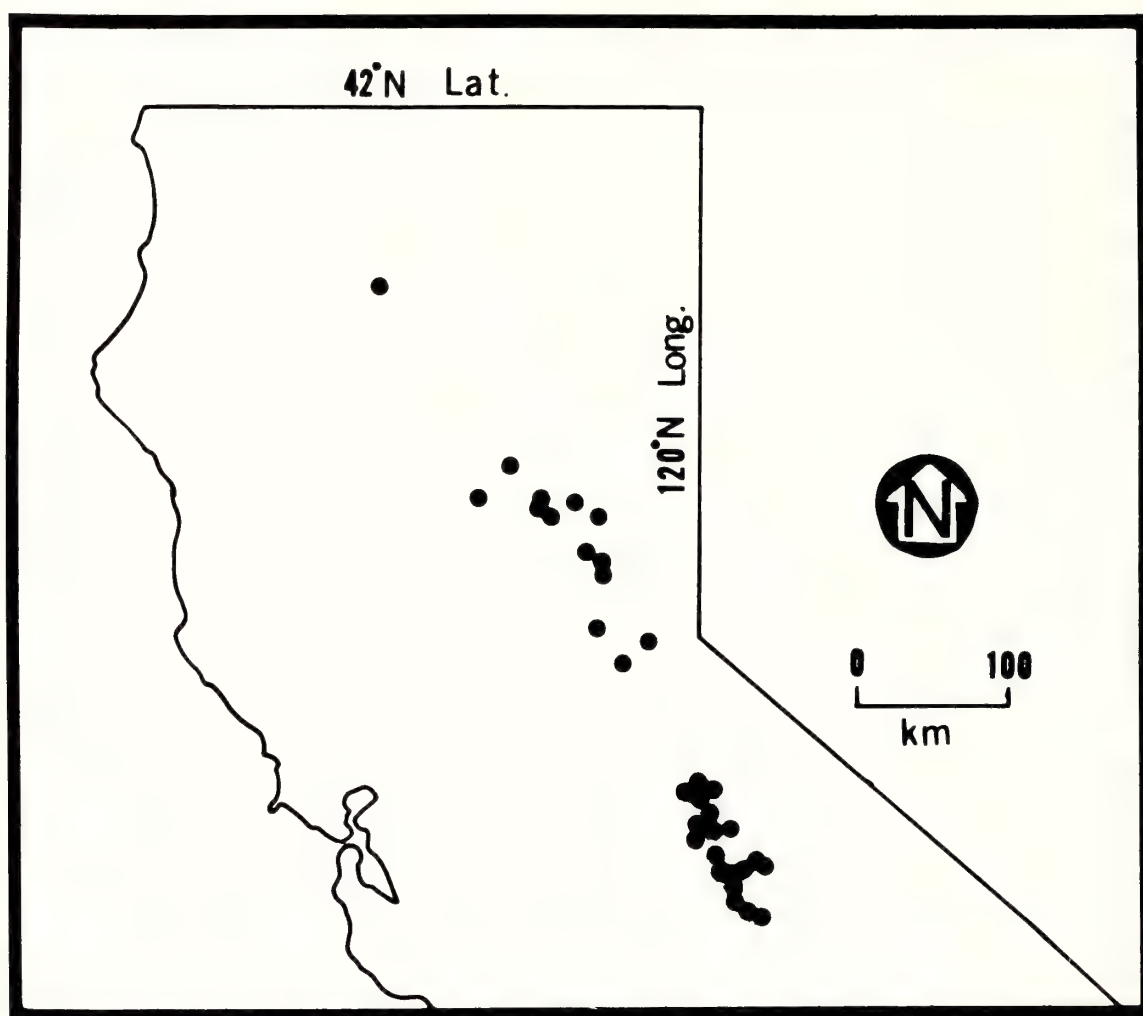


FIG. 1. Distribution of *Phacelia vallicola* Congdon. ex Brand. Locations based on herbarium specimens and the literature.

due to logging of adjacent lands. The rock outcrops and talus slopes that support *Phacelia vallicola* support a sparse cover of trees and thus are not prime timber lands.

*Significance.* Mariposa phacelia, *Phacelia vallicola*, is currently on the watch list of the inventory of California's rare and endangered plants [Smith and Berg, CNPS Spec. Publ. No. 1, 4th ed., 1988]. Based on the presented range extension and wide habitat requirements, *Phacelia vallicola* is too widespread to be considered a plant of concern.

Based on the current knowledge of this plant's distribution, Mariposa phacelia would more appropriately be called Congdon's phacelia. J. W. Congdon, a physician in the foothill mining town of Mariposa and an active plant collector, discovered the plant in the late 1800's.

I thank Dr. Gregory Lee for verifying the identifications of several specimens. Thanks also goes to Carrie Anne Shaw for assistance in the San Francisco Bay Area herbaria and to the curators of the cited institutions for access to specimens.—FREDERICA S. BOWCUTT, California Dept. of Parks and Recreation, Box 942896, Sacramento, CA 94296-0001. (Received 5 Oct 1988; revision accepted 4 Nov 1988.)



## NOTEWORTHY COLLECTIONS

### CALIFORNIA

*PALLAVICINIA LYELLII* (Hook.) S. Gray (HEPATICAE: PALLAVICINIACEAE). — Humboldt Co., Arcata, 0.5 mi up Jolly Giant Creek from Humboldt State University dormitories, in a moist recess of a rotten log, next to a creek, in a second growth redwood forest, T6N R1E sect. 28, 100 m, 2 Oct 1987, *Wilson 1534* (NY, ORE confirmed D. H. Wagner).

*Significance.* A species common in eastern North America; the nearest previously published record came from Minnesota. The new site is removed from present human activities and disturbances, providing no reason to assume that the plant's presence is the result of a recent anthropogenic introduction. — PAUL WILSON, Department of Ecology and Evolution, State University of New York, Stony Brook, NY 11794.

### CALIFORNIA

*PENSTEMON VENUSTUS* Douglas ex Lindley (SCROPHULARIACEAE). — Lassen Co., Sierra Nevada, SW side of Fredonyer Butte; on several roadcuts along CA hwy 36 through Susan River alluvium in pineland ca. 11.5 mi (18.5 km) WSW of Susanville, T29N R10E sect. 15, ca. 5200 ft (1585 m), collected in flower 25 Jun 1987, *Vincent 4436* (NY), and in fruit 5 Aug 1987, *Vincent 4500* (NY).

*Significance.* First report for CA. Observed first in 1986, ca. 30 individuals were seen in 1987 on two roadcuts, so presumably naturalized. Native to drainages of the Columbia and Snake rivers of adjacent WA, OR, and ID, often on similar alluvial soils. — KARL A. VINCENT, New York Botanical Garden, Bronx, NY 10458.

### OREGON

*ASTRAGALUS CURVICARPUS* (Sheldon) Macbride var. *SUBGLABER* (Rydb.) Barneby (FABACEAE). — Baker Co., W side of Powder River Canyon, NE of Baker in recently burned *Artemisia tridentata*/*Festuca idahoensis*-*Agropyron spicatum* community (T7S R40E sect. 13?), ca. 300 m, 19 Jun 1985, *E. Joyal 883* (Baker-BLM, NY, OSC). (Verified by R. Barneby, NY.)

*Significance.* Extension E of ca. 150 km from the lower Deschutes and John Day River drainages.

*COLLOMIA DEBILIS* (S. Watson) E. Greene var. *LARSENII* (A. Gray) Brand (POLEMONIACEAE). — Grant Co., Wallowa-Whitman Natl. For., Elkhorn Crest trail S of Anthony Lake, common in talus along trail (T7S R37E sect. 30?), ca. 2500 m, 1 Sep 1985, *E. Joyal 1030* (CS, OSC). (Verified by D. Wilken, CS.)

*Significance.* Extension E of ca. 300 km from the Cascade Range of Oregon.

*RUDBECKIA OCCIDENTALIS* Nutt. var. *MONTANA* (A. Gray) Perdue (ASTERACEAE). — Baker Co., Elkhorn Range, Hunt Mt., Pine Cr., common along stream bank in *Pseudotsuga menziesii* forest opening (T8S R38E sect. 21), ca. 1700 m, 23 Jul 1985, *E. Joyal 1004* (OSC); 20 Jul 1986, *E. Joyal 1225* (Baker-BLM, CAS, NY, OSC, UTC). (Verified by A. Cronquist, NY.)

*Significance.* First record for OR and an extension NW of ca. 900 km from S UT and W CO. — ELAINE JOYAL, The Nature Conservancy, 1815 N. Lynn St., Arlington, VA 22209.



## REVIEWS

*Guide to the Regional Parks Botanic Garden.* By WALTER KNIGHT with IRJA KNIGHT. East Bay Regional Park District, 11500 Skyline Blvd., Oakland, CA 94619-2443. 1988. 490 pp., Soft cover. \$20.00.

Any walk through the East Bay Regional Parks Botanic Garden at Tilden Park in Berkeley, CA is a delight. However, if you seek a particular taxon then the new revision of *Guide to the Regional Parks Botanic Garden* provides a valuable assist. Hereafter, I will refer to the revision as the Guide.

The garden is divided into ten sections representing major botanic regions of California. The planted beds in each section are identified by color coded stakes. Individual plants are labeled with the same sectional color and also by number (e.g., the SIERRAN plants in Section 6 are in Bed numbers 601–662 and are color coded Blue).

The Guide includes a California map illustrating the general location of the ten major botanic regions. A map of the Botanic Garden helps you to find a specific section in the garden. Inconveniently, these two important maps are 32 pages apart. The first 38 pages are numbered by Roman Numerals; the remaining pages of the Guide are not numbered. Access to the plant data is provided by an index at the end of the text.

The index, nicely highlighted by buff-colored pages, is an alphabetical listing of scientific and common names, the latter in bold face. I would have preferred the scientific names to be bold face type. Numbers following the names refer to bed numbers in the several sections (e.g., *Ceanothus roderickii* 610, 647).

Bed 647 contains eight species including 84.320 *Ceanothus roderickii* Knight. PINE HILL CEANOTHUS. The number 84.320 means that this specimen was the 320th acquisition made in 1984. Other data include: family name, rare & endangered status, location, habitat, flowering time, morphology, habit, and county. I tested the accuracy of the Guide by locating many plants and found no errors in my test sample.

Besides the ten major sections there are three special habitats: the ANTIOCH DUNES area (yellow labels), the COASTAL DUNES area (yellow labels), and the POND area (small brown labels). White labels either indicate self-sown plants native to the park or plants not native to California.

The Guide begins with pertinent “General Information” and a good “Using the Guide” portion. Also included are “more history”, reports, a weed list, literature cited, Indian (Native American) culture literature, glossary, and illustrations of plant structural attributes. If the editors of a future revision would place much of the supporting information in appendices, then the two critical maps would be together. This would make the Guide even more effective.

The East Bay Regional Parks Botanic Garden is a beautiful, functional asset to those of us who enjoy plants. The *Guide to the Regional Parks Botanic Garden* greatly enhances the value of the garden. —CLIFFORD L. SCHMIDT, Department of Biological Sciences, San Jose State University, San Jose, CA 95192-0100.

*Inventory of Rare and Endangered Vascular Plants of California.* Edited by JAMES P. SMITH and KEN BERG, illustrated by LORAN MAY. California Native Plant Society, Special Publication Number One (4th ed.), Sacramento. Sep. 1988. 168 pp. Softbound. \$19.95.

The California Native Plant Society has, since its inception in the 1960's, been “Dedicated to the Preservation of California Native Flora”. A central feature of this



dedication was, and is, the listing of plants that are threatened in some way. Starting with a card file of G. Ledyard Stebbins the society began to develop lists of Rare and/or Endangered Plants. These were, at first, informal lists, but by 1974 they had been refined to the point that they were incorporated into the first edition of the *Inventory*. This first edition was edited by W. Robert Powell and was made possible by the contributions of time and talent by many professional and lay botanists. A number of eminent botanists were invited to join a Scientific Advisory Committee, while others combed herbaria and searched for the plants in the field. This *Inventory* quickly became the source book for anyone who needed information about endangered plants.

An edition of the *Inventory* is based on the best information available at the time of publication. Therefore the subsequent editions have been evolutionary rather than revolutionary in nature. This undertaking of the Native Plant Society was the first of its kind. It became evident at the map-in of 1974 that information was entirely lacking or incomplete for many taxa throughout the state. It was six years before the backlog of information became so great that it was necessary to publish the second edition, although supplementary lists had been circulated.

The hiring of a staff botanist and the acquisition of a computer made it easier for the society to perfect the lists. In fact there were a couple of supplements between the second edition of 1980 and the third edition of 1984. Supplements were not published between the third and fourth editions.

Why publish a new edition now? Taxa formerly thought to be extinct have been rediscovered. Some thought to be rare were determined to be fairly common. Other taxa that were once found in relatively large numbers are now presumed to be extinct or nearly so. Many field studies have been undertaken under the direction of the several agencies involved with data collection. These have been done by volunteers, many of whom have been giving of their time and expertise since the beginning of the program. A number of experts in certain taxa have had time to complete studies which have resulted in changes of one kind or another.

The resulting informational changes have been incorporated into the new edition. Changes in format have also been made. The one most obvious change has been made possible through the acquisition of computer software. It allows the society to convert data files to camera-ready copy which is produced in two columns with the type across the short dimension of the page. That is, the text may be read with the book held upright. Previous editions have had the data for each taxon spread across the length of the page. This change should meet with universal approval.

A change which may prove more controversial is the incorporation of all the lists into one unit. This unit includes all taxa considered, in an alphabetical sequence. The lists are still the same: #1A, Presumed extinct in California; #1B, Rare or endangered in California and elsewhere; #2, Rare and endangered in California, more common elsewhere; #3, Need more information; #4, Plants of limited distribution, a watch list. The assembled lists appear in Appendix II as long, continuous, alphabetical listings of scientific names only.

When one needs to find a certain taxon, this arrangement of the taxa into one unit has certain advantages. Any taxon may be found easily, regardless of its listing. There are even plants in the main body which have been considered but rejected because they did not warrant inclusion in one of the lists.

There are a few other minor changes. Edition 3 had each botanical name written entirely in upper case. Edition 4 returns to properly written scientific names using italics. The strategically placed drawings of Loran May enhance the appearance of the text, and the Prisma Color Pencil drawing of Barbara Adair makes this cover the most beautiful one yet.

The book is very well edited. I found only a few very minor typographical errors. The new type-setting capabilities have improved the appearance of the text. Even last minute changes in the data have been incorporated. All in all the book reflects the many hours of work which have gone into its production. The editors, the many contributors and the Native Plant Society may be justly proud of the results of their



efforts.—MALCOLM G. MCLEOD, Biological Sciences Department, California Polytechnic State University, San Luis Obispo, CA 93407.

*Colorado Flora: Western Slope.* By WILLIAM A. WEBER. Colorado Associated University Press, Boulder, CO. 1987. 530 pp. Hardbound. \$19.50. ICBN 0-87081-167-3.

This handy-sized field guide is an expression of the author's broad knowledge of plants worldwide and years of field experience. The format is easy to use by the amateur (or the professional) and includes a glossary, 64 color plates and more than 100 line drawings. The flora includes all vascular plants (ferns and fern allies, gymnosperms, and angiosperms) of the "entire hydrologic Western Slope of Colorado—from the Continental Divide to the Utah, Wyoming, and New Mexican borders." Each major group is presented in alphabetical sequence, in turn, by family, genus, and species. Families bear descriptions, but lower level taxa are mostly described only in the keys.

This guide is very similar to its earlier version, *The Rocky Mountain Flora* (Weber, W. A., 1972, Colorado Assoc. Univ. Press, Boulder), but now includes more taxa in its larger geography, more numerous and better detailed illustrations, and more realistic family treatments of ferns and gymnosperms. The generic treatment will probably disturb certain users. Many genera have been subdivided (even more so than in the earlier version), apparently due to the author's belief in narrow generic concepts and his worldwide knowledge of certain plant groups. He may be justified for these changes, but for those familiar with floras of the surrounding states, many new generic names will be hard to translate because the full direct synonyms used in the earlier version are no longer present; usually there is only a note to indicate in which genus it was formerly included. I believe that it is the duty of the author to defend the position (however correct) from commonly used scientific names.

In general, I am much concerned about the diverse treatments of generic circumscription by taxonomists. Obviously the taxonomist must have freedom of expression and judgement, but I am concerned when certain genera are split and reunited repeatedly generation after generation. One suggestion might be that generic delimitation should (must?) include major differences in reproductive structures, not to be distinguished by vegetative characters alone, e.g., *Berberis* vs. *Mahonia*; *Euphorbia* vs. *Chamaesyce*, *Poinsettia*, etc.; *Fouquieria* vs. *Idria*; *Potentilla* vs. *Argentina*; *Opuntia* vs. *Cylindropuntia*; and so on.

I recommend this flora despite nomenclature inconveniences; the book size is right; the quality is good, and the price is right.—DONALD J. PINKAVA, Department of Botany, Arizona State University, Tempe, AZ 85287-1601.

*Trees and Shrubs of Trans-Pecos Texas.* By A. MICHAEL POWELL. 1988. Big Bend Natural History Association, Big Bend National Park, TX. 536 pp. \$19.95 (paperbound) ISBN 0-912001-14-3.

*Trees and Shrubs of Trans-Pecos Texas* is a complete and professional treatment of the woody plants west of the Pecos River in Texas. It begins with a short description of the area, including climate, soils, topography, and major vegetation types. A map of the counties and major topographic features clearly defines the area covered in the manual. Each of the five vegetation types in the Trans-Pecos is described using both common and scientific names for the dominant plant species and illustrated with photographs. The introduction is followed by a floristic treatment that includes keys to families, genera, and species as well as family and generic descriptions. Species accounts consist of fairly detailed distribution information and usually some interesting facts about the plant, ranging from economic uses to newly discovered localities. Most species are illustrated in fine pen and ink drawings showing vegetative, floral, and fruiting features. Common names and a short glossary are provided to aid novices.

The manual is quite comprehensive and includes many slightly woody perennial herbs in addition to trees and shrubs. The nomenclature is up to date with only a



few exceptions (e.g., *Petalostemum*, a genus that Barneby sank into *Dalea* in 1977, is discussed as being poorly differentiated from *Dalea*). The dichotomous key to families is indented, easy to read, and numbered such that it is very easy to backtrack. This is a big advantage because my major criticism of the book is that Powell borrowed the family key from Correll and Johnston's *Manual of the Vascular Plants of Texas*. This key can be notoriously difficult and, while we are spared the "not as above" couplets, the dreaded "spirally coiled embryo" couplet still must be traversed to arrive at the Chenopodiaceae. Generic and species keys are much better, probably because many of them are tailored for the Trans-Pecos.

The illustrations are very good and might make up for the defects in the key as one can leaf through the manual looking for the plant in question. A remarkable number of the species are illustrated (the Agavaceae and Cactaceae with photographs rather than line drawings) and although the drawings have been reduced in size to conserve space, the salient features can still be seen.

There are many small errors scattered throughout the text and the book would have benefited from more careful editing. Thus, we find *Cercocarpus* is misspelled as *Cercocarcarpus*, Figures 2 and 3 in the introduction seem to have been switched, and *Krameria parvifolia* is found in every country rather than county.

In his preface, Powell states that the book is intended for use by both scientists and non-scientists. It is obvious that he has made a serious attempt to avoid overusing technical terminology and to include common names. As a consequence, both the introduction and floristic treatments are eminently readable. Were it not for the family key, I would whole-heartedly recommend the book to any amateur botanist. The book is handsomely bound with a durable plastic-coated cloth cover and sewn pages and should withstand many seasons in the field. *Trees and Shrubs of Trans-Pecos Texas* is a valuable addition to the growing body of regional floras and will be a useful tool for all those interested in this beautiful and fascinating area.—MELISSA LUCKOW, Department of Botany, University of Texas, Austin, TX 78713.

*A Guide to Wildlife Habitats of California*. K. E. MAYER and W. F. LAUDENSLAYER, JR. (eds.). 166 pp., paperbound. California Department of Forestry and Fire Protection, Sacramento. 1988. Copies may be obtained from WHR Coordinator, Department of Fish and Game, 1701 Nimbus Road, Suite D, Rancho Cordova, CA 95670. \$13.02 including tax and shipping.

This is the first of several publications from the California Wildlife-Habitat Relationships (WHR) System designed to serve as ecosystem-oriented resources for wildlife biologists and managers in California. The *Guide* describes various wildlife habitats that constitute the WHR classification system that was developed by the California Interagency Wildlife Task Group. Its goal is to identify and classify existing vegetation types important to wildlife. One objective of the WHR system is to address the problem of confusion among vegetation/habitat-type classifications prepared for different purposes (e.g., wildlife biology, range management, forestry, etc.) by providing a framework that can be used by all. The introduction describes the purposes for which the book has been designed, how it was constructed, and how it is to be used. It includes a tabular comparison of the WHR classification with others published for California vegetation. Contributions by various specialists have been tightly edited for standardization of format and information content. "Habitats" (communities) are grouped as "Tree-dominated," "Shrub-dominated," "Herbaceous-dominated," "Aquatic," and "Developed."

The one- to two-page written summary of each habitat type begins with "Vegetation," a section broken into paragraphs on structure (physiognomy), composition including dominants and major associated species, and a comparison of other classification schemes. A section entitled "Habitat Stages" is a summary of current knowledge (often very little) about successional relationships. The "Biological Setting" includes a brief description of "habitat" that lists ecotonal relationships of the habitat



type being described and “wildlife considerations” that summarizes the importance of the community to wildlife. “Physical Setting” describes the characteristics of the physical environment within which the habitat type occurs. “Distribution” includes a paragraphic summary with geographical range and elevational zonation. A map depicts the community’s distribution or potential distribution in California. Some maps are much more generalized than others; for instance, the distribution of the “Blue-oak” habitat type is broken into many tiny patches whereas that of “Joshua Tree” is a single large blotch that includes many areas where this species does not occur. There is a single high-resolution color photograph of each community. Line drawings of various birds, mammals, reptiles, and amphibians that occur in California are dispersed through the text, generally one per community; these do not appear to be indexed in any way.

A curious feature of the WHR classification is the unevenness of “habitat” definition. This is noted in the introduction as a “Caveat for Users,” but the rationale for the differences in inclusiveness is not always readily apparent. For example, “Blue Oak” is treated as a separate habitat from “Blue Oak-Digger Pine” though the two intergrade extensively and share the same suite of associates. On the other hand, “Coastal Scrub” is defined so broadly that communities with no species in common at all are included together. Within “Coastal Scrub” the plants of beaches and dunes are grouped together with species of other very different environments and are not even mentioned in the community discussion. One would hope that management practices for dune communities would be different from those of areas with more stable substrates and different ecological constraints. A “habitat” entitled “Chamise-Redshank Chaparral” is depicted as occurring throughout most of cismontane California although redshank (*Adenostoma sparsifolium*) is found no farther north than San Luis Obispo County and forms communities quite different in physiognomy and stature than chamise (*Adenostoma fasciculatum*).

The book has a collective “Literature Cited” section. Common names are used in the text, and are cross-referenced to species names in a “Species List” at the end of the book. This is a one-way cross-reference; a user who knows a species name but not the common name can spend a lot of time looking. Additionally, some common names are of peculiar derivation, and may not be the names used commonly by people in the field—always a problem with common names. A shortfall of the book is the lack of an index.

Despite its shortcomings, the *Guide* is sure to be a useful addition to the information available to wildlife biologists and wildlife managers. The price is very affordable. I hope that the editors will readily accept input from the botanical community and prepare a revised edition before too much time has passed. — DAVID J. KEIL, Biological Sciences Department, California Polytechnic State University, San Luis Obispo, CA 93407.



## ANNOUNCEMENT

### NEW PUBLICATIONS

- ALBEE, B. J., L. M. SHULTZ, and S. GOODRICH. 1988. *Atlas of the vascular plants of Utah*. 670 pp. ISBN 0-940378-09-4. Utah Museum of Natural History, Salt Lake City, UT 84112. \$26.00 (clothbound) + \$4.00 shipping and handling. [The atlas includes distribution data in the form of dots on detailed relief maps for each of the 2438 species growing in Utah in more than one location and without benefit of cultivation. Data for the publication were obtained by critical examination of some 400,000 specimens housed in the various herbaria in Utah. Phenological and ecological data are provided for each species, an annotated list of 384 species restricted in distribution is included in an appendix, and alternate scientific names are provided in the index.]
- BOWERS, J. E. 1988. *A sense of place. The life and work of Forrest Shreve*. University of Arizona Press, 1230 N. Park, #102, Tucson, AZ 85719. \$19.95 (clothbound). [A biography of pioneer plant ecologist, Forrest Shreve, whose work laid the foundation for many subsequent ecological studies in western North America.]
- BURBRIDGE, J. 1989. *Wildflowers of the southern interior of British Columbia and adjacent parts of Washington, Idaho, and Montana*. 400 pp., approx. ISBN 0-7748-0320-7. University of British Columbia Press, 6344 Memorial Road, Vancouver, B.C. V6T 1W5, Canada. \$29.95 (clothbound) or \$19.95 (paperbound) + postage and handling (\$1.60 in Canada; \$3.50 in the U.S.). [A field guide illustrated with 335 color photographs, diagrams, and 1 map.]
- FERREN, W. R. and D. A. PRITCHETT. 1988. *Enhancement, restoration, and creation of vernal pools at Del Sol Open Space and Vernal Pool Reserve, Santa Barbara County, California*. Environmental Research Team, The Herbarium, Department of Biological Sciences, University of California, Santa Barbara, CA 93106. Environmental Report No. 13. 169 pp. plus two booklets. \$15.00 (paperbound).
- KLINKA, A., V. J. KRAJINA, A. CESKA, and A. M. SCAGEL. 1989. *Indicator plants of coastal British Columbia*. 330 pp., approx. ISBN 0-7748-0321-5. University of British Columbia Press, 6344 Memorial Road, Vancouver, B.C. V6T 1W5, Canada. \$36.95 + postage and handling (\$1.60 in Canada; \$3.50 in the U.S.). [419 selected vascular plants, bryophytes, and lichens of coastal British Columbia are described and illustrated in color. Indicators with similar values are grouped into indicator species groups that are used to evaluate site quality. Information is presented on geographical distribution, life-form, shade tolerance, and other ecological characteristics. Three methods are presented for use of indicator plants for site diagnosis.]



## ANNOUNCEMENT

### MINOR CHANGES IN MADROÑO FORMAT

In response to comments from authors and reviewers, I polled past Editors, and members of the Editorial Board regarding various editorial matters. Beginning with this issue, readers will see several minor stylistic changes in *Madroño*'s format that resulted from the various comments. The changes are summarized below.

For mailing addresses within the United States, the postal abbreviation of the state will be included whether the name of the state is mentioned in the institutional title or not. Postal abbreviations will also be used in specimen citations, except in the case of types where the name of a state will be spelled out in full.

To the extent possible, citation of authors for scientific names will follow the *Draft index of author abbreviations* compiled at the Royal Botanic Gardens at Kew (1980). Authors who do not have access to a copy of the *Draft index* should note this in the cover letters with their manuscript submissions to alert the Editor to non-standard author abbreviations. In adopting the *Draft index* as a standard, *Madroño* joins *Systematic Botany* and the *Jepson Manual Project* among others.

There is a minor change in punctuation of literature citations within the text of an article where two or more papers are cited together. Examples of the new style follow: (Jones 1976, 1977), (Jones 1976; Smith 1987), (Jones 1976, 1977a, b; Smith 1987). Note the use of semicolons where commas formerly appeared.

Citation of nomenclatural types has been somewhat inconsistent in the past. Type citations will now appear immediately after the names that they typify and before the diagnosis and/or description of the taxon (as on p. 18, this issue). In all cases the specific kind of type will be used; the word "holotype," for instance, will be used and not implied by the word "type." Unless the reasons for lectotype choice are particularly complicated, the rationale for lectotypification will accompany the type citation.

Dichotomous keys now appear in 8-point type (as on p. 31, this issue) instead of 10 point. Compass directions now appear as capital letters without punctuation rather than as lower case with punctuation.

Observant readers may note a few other changes that are not mentioned here. I apologize in advance to authors whose manuscripts are caught in the transition. —DAVID J. KEIL, *Editor*.



## SUBSCRIPTIONS—MEMBERSHIP

Membership in the California Botanical Society is open to individuals (\$22 per year; students \$12 per year for a maximum of seven years). Members of the Society receive MADROÑO free. Family memberships (\$25) include one five-page publishing allotment and one journal. Emeritus rates are available from the Corresponding Secretary. Institutional subscriptions to MADROÑO are available (\$30). Membership is based on a calendar year only. Applications for membership (including dues), orders for subscriptions, and renewal payments should be sent to the Treasurer. Requests and rates for back issues, changes of address, and undelivered copies of MADROÑO should be sent to the Corresponding Secretary.

## INFORMATION FOR CONTRIBUTORS

Manuscripts submitted for publication in MADROÑO should be sent to the editor. All authors must be members, and membership is prerequisite for review.

Manuscripts and review copies of illustrations must be submitted in triplicate for all articles *and* short items intended for NOTES AND NEWS. Follow the format used in recent issues for the type of item submitted and allow ample margins all around. All manuscripts **MUST BE DOUBLE SPACED THROUGHOUT**. For articles this includes title (all caps, centered), author names (all caps, centered), addresses (caps and lower case, centered), abstract, text, acknowledgments, literature cited, tables (caption on same page), and figure captions (grouped as consecutive paragraphs on one page). Order parts in the sequence listed ending with figures, and number each page. Do not use a separate cover page, "erasable" paper, or footnotes. Manuscripts prepared on dot matrix printers may not be considered. Table captions should include all information relevant to tables. All measurements should be in metric units.

Line copy illustrations should be clean and legible, proportioned (including captions) to the MADROÑO page, and designed for reduction to  $\frac{2}{3}$  original size. Scales should be included in figures, as should explanation of symbols, including graph coordinates. Symbols smaller than 1 mm after reduction are not acceptable. Maps must include latitude and longitude references. Halftone copy should be designed for reproduction at actual size. In no case should original illustrations be sent prior to the acceptance of a manuscript. When needed they should be mounted on stiff cardboard and sent flat. No illustrations larger than 22 × 28 cm will be accepted.

Presentation of nomenclatural matter (accepted names, synonyms, typification) should follow the format used for *Rhus integrifolia* in MADROÑO 22:288. 1974. Institutional abbreviations in specimen citations should follow Holmgren, Keuken, and Schofield, Index Herbariorum, 7th edition. Abbreviations of serial titles should be those in Botanico-Periodicum-Huntianum (Lawrence et al., 1968, Hunt Botanical Library, Pittsburgh). If the correct abbreviation cannot be determined, the full serial title should be used. Titles of books should be given in full, together with the place and date of publication, publisher, and edition, if other than the first.

All members of the California Botanical Society are allotted five free pages per volume in MADROÑO. Joint authors may split the full page number. Beyond that number of pages a required editorial fee of \$65.00 per page will be assessed. The purpose of this fee is not to pay directly for the costs of publishing any particular paper, but rather to allow the Society to continue publishing MADROÑO on a reasonable schedule, with equity among all members for access to its pages. Printer's fees for illustrations and typographically difficult material @ \$35.00 per page (if their sum exceeds 30 percent of the paper) and for author's changes after typesetting @ \$4.50 per line will be charged to authors.

At the time of submission, authors must provide information describing the extent to which data in the manuscript have been used in other papers that are published, in press, submitted, or soon to be submitted elsewhere.





## CALIFORNIA BOTANICAL SOCIETY

### STATEMENT OF OWNERSHIP, MANAGEMENT, AND CIRCULATION

(Required by Title 39, U.S.C. 3685)

MADROÑO, A West American Journal of Botany, is published quarterly at Berkeley, California. Annual subscription price is \$25.00.

The Publisher is the California Botanical Society, Inc., Life Science Building, University of California, Berkeley, CA 94720.

The editor is David J. Keil, Biological Sciences Department, California Polytechnic State University, San Luis Obispo, CA 93407.

The owner is the California Botanical Society, Inc., Life Science Building, University of California, Berkeley, CA 94720. There are no bondholders, mortgagees, or other security holders.

The average number of copies distributed of each issue during the preceding 12 months is 1108; the number of copies of the single issue closest to the filing date is 1132. The net press run is 1250 copies.

I certify that the statements made by me above are correct and complete.

24 February 1989

DAVID J. KEIL, *Editor*



83  
7.

## MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

## Contents

|  |     |
|--|-----|
| FLORA OF THE SIERRA DE LA LAGUNA, BAJA CALIFORNIA SUR, MEXICO<br><i>Jose Luis León de la Luz and Raymundo Domínguez-Cadena</i>                                     | 61  |
| ECOLOGY AND DISTRIBUTION OF <i>PINUS LAGUNAE</i> IN THE SIERRA DE LA LAGUNA, BAJA CALIFORNIA SUR, MEXICO<br><i>Marie-François Passini and Nicole Pinel</i>         | 84  |
| POSTFIRE VEGETATION DEVELOPMENT IN THE COSTA RICAN PARAMOS<br><i>Sally P. Horn</i>   | 93  |
| A NEW SPECIES OF <i>ERIGERON</i> (ASTERACEAE: ASTEREAE) FROM CENTRAL NEW MEXICO<br><i>Richard Spellenberg and Paul Knight</i>                                      | 115 |
| A RE-EVALUATION OF THE <i>ALLIUM SANBORNII</i> (ALLIACEAE) COMPLEX<br><i>Stella S. Denison and Dale McNeal</i>   | 122 |
| NOTES  |     |
| <i>MYOSOTIS LATIFOLIA</i> AND NOT <i>M. SYLVATICA</i> (BORAGINACEAE) IN CALIFORNIA<br><i>Elaine Joyal</i>  | 131 |
| MOONWORTS ( <i>BOTRYCHIUM</i> : OPHIOGLOSSACEAE) IN THE JONESVILLE AREA, BUTTE AND TEHAMA COUNTY, CALIFORNIA<br><i>Warren H. Wagner, Jr. and Timothy B. Divine</i> | 131 |
| <i>SALIX SCOULERIANA</i> J. BARRATT EX HOOK. (SALICACEAE) IN SONORA, MEXICO<br><i>George W. Argus</i>  | 135 |
| TYPIFICATION OF <i>SALIX GEYERIANA</i> (SALICACEAE)<br><i>Robert W. Dorn</i>   | 135 |
| NOTEWORTHY COLLECTIONS   |     |
| ARIZONA  | 136 |
| COMMENTARY   |     |
| POINTS OF VIEW: ON THE MODERN DEATH OF DAVID DOUGLAS<br><i>James L. Reveal</i>   | 137 |
| ANNOUNCEMENTS  |     |
| TEMPORARY NEW ADDRESS FOR EDITOR OF MADROÑO  | 121 |
| NEW PUBLICATIONS   | 140 |



MADROÑO (ISSN 0024-9637) is published quarterly by the California Botanical Society, Inc., and is issued from the office of the Society, Herbarium, Life Sciences Building, University of California, Berkeley, CA 94720. Subscription rate: \$30 per calendar year. Subscription information on inside back cover. Established 1916. Second-class postage paid at Berkeley, CA, and additional mailing offices. Return requested. POSTMASTER: Send address changes to James R. Shevock, Botany Dept., California Academy of Sciences, San Francisco, CA 94118.

*Editor*--DAVID J. KEIL  
Biological Sciences Department  
California Polytechnic State University  
San Luis Obispo, CA 93407

*Board of Editors*

Class of:

- 1989--FRANK VASEK, University of California, Riverside, CA  
BARBARA ERTTER, University of California, Berkeley, CA  
1990--STEVEN TIMBROOK, Ganna Walska Lotusland Foundation, Montecito, CA  
THOMAS R. VAN DEVENDER, Arizona-Sonora Desert Museum, Tucson, AZ  
1991--JAMES HENRICKSON, California State University, Los Angeles, CA  
WAYNE R. FERREN, JR., University of California, Santa Barbara, CA  
1992--BRUCE A. STEIN, The Nature Conservancy, Washington, D.C.  
WILLIAM L. HALVORSON, Channel Islands National Park, Ventura, CA  
1993--JON E. KEELEY, Occidental College, Los Angeles, CA  
RHONDA L. RIGGINS, California Polytechnic State University, San Luis Obispo, CA

---

CALIFORNIA BOTANICAL SOCIETY, INC.

OFFICERS FOR 1988-89

- President:* JOHN L. STROTHER, University Herbarium, University of California, Berkeley, CA 94720  
*First Vice President:* JAMES AFFOLTER, Botanical Garden, University of California, Berkeley, CA 94720  
*Second Vice President:* JAMES HENRICKSON, California State University, Los Angeles, CA 90032  
*Recording Secretary:* RODNEY G. MYATT, Department of Biological Sciences, San Jose State University, San Jose, CA 95192  
*Corresponding Secretary:* JAMES R. SHEVOCK, Department of Botany, California Academy of Sciences, San Francisco, CA 94118  
*Treasurer:* THOMAS F. DANIEL, Department of Botany, California Academy of Sciences, San Francisco, CA 94118  
*Financial Officer:* CHERIE L. WETZEL, Department of Biology, City College of San Francisco, 50 Phelan Ave., San Francisco, CA 94112

The Council of the California Botanical Society consists of the officers listed above plus the immediate *Past President*, DALE MCNEAL, Department of Biological Sciences, University of the Pacific, Stockton, CA 95211; the *Editor* of MADROÑO; three elected *Council Members*: JOHN MOORING, Department of Biology, University of Santa Clara, Santa Clara, CA 95053; BARBARA ERTTER, Herbarium, Botany Department, University of California, Berkeley, CA 94720; ELIZABETH MCCLINTOCK, Herbarium, Botany Department, University of California, Berkeley, CA 94720; and a *Graduate Student Representative*, VALERIE HALEY, Department of Biological Sciences, San Jose State University, San Jose, CA 95192.

|   |
|---|
| THIS PUBLICATION IS PRINTED ON ACID-FREE PAPER. |
|---|



## FLORA OF THE SIERRA DE LA LAGUNA, BAJA CALIFORNIA SUR, MEXICO

JOSÉ LUIS LEÓN-DE LA LUZ and RAYMUNDO DOMÍNGUEZ-CADENA  
Centro de Investigaciones Biológicas de Baja California Sur,  
Apdo. Postal 128, La Paz, Baja California Sur, México

### ABSTRACT

The Sierra de la Laguna is the main high mountain range in the southern portion of the arid state of Baja California Sur (Mexico). It is high and narrow, rising boldly from coastal lowlands, with many precipitous and rocky slopes. Its peaks reach up to 2200 m. Above 1500 m the Sierra is occupied by the only montane woodland community in the state and it is believed to have been an island in both the strict and biological senses. Our botanical survey in the oak-pine woodland community of the Sierra de la Laguna, between 1982 and late 1987, reports 66 families of vascular plants, including 228 taxa. These are distributed in four groups by habit: 8% are trees, 10% are shrubs or subshrubs, 43% are short-lived perennial herbs, and 14% are hydrophytes. About 17% of this flora may be considered endemic. Almost a century ago, a survey in approximately the same area (by T. S. Brandegee) yielded 146 taxa of vascular plants. The main purpose of this study is to document botanical resources in support of the establishment of this plant community as a preserve, in accordance with some MAB-UNESCO fundamentals.

### RESUMEN

La Sierra de la Laguna se ubica en la porción más elevada de las montañas del sur del árido estado de Baja California Sur (México). La serranía se eleva sobre de una inmensa planicie costera y se caracteriza por lo pronunciado de sus declives. Las cimas alcanzan hasta 2200 m de altitud. Por encima de los 1500 m se encuentra la única comunidad propiamente boscosa de la entidad, entre ésta y los 1000 m se ubica un encinar; ésta comunidad puede ser considerada como una isla tanto en el sentido estricto como biológico. Las exploraciones efectuadas han rendido hasta la fecha 228 especies de plantas vasculares comprendidas en 66 familias. Estas se han ubicado en las siguientes formas de vida: 8% árboles, 10% arbustos o subarbustos, 43% de herbáceas, y 14% de hidrófitas. Casi el 17% de la flora considerada es endémica. Hace casi un siglo T. S. Brandegee realizó una investigación florística en la misma área reportando sólo 146 taxa. El objetivo central de este trabajo consiste en actualizar el conocimiento florístico de la serranía en referencia, actualmente en vías de decretarla como una Reserva de la Biósfera de acuerdo con los planteamientos de MAB-UNESCO.

The flora of the Baja California peninsula has been the concern of American botanists for over a century and a half. Early collections were made by J. Xantus, L. Belding, T. S. Brandegee, C. A. Purpus, E. A. Goldman, and many others (Johnson 1958). Recent publications include those of Shreve and Wiggins (1964), Wiggins (1980), and Gould and Moran (1981). During the present century, several California botanists have contributed greatly to our knowledge of



the peninsular flora: M. E. Jones, A. Eastwood, I. M. Johnston, R. Moran, and A. Carter. Most of these investigations have focused on the central and northern areas of Baja California.

In the southern tip of the peninsula, botanical explorations have been rare. This area was designated as a biogeographical unit by Bryant (1891) as "Cape Region of Baja California". Nelson (1921) and Shreve (1937) published early botanical descriptions of the arid and tropical portions of the region. More recently, Gilmartin and Neighbours (1978) undertook field work in hopes of preparing a flora of this region, but their project was never completed.

Within the Cape Region, the Sierra de la Laguna resembles an island. A vegetation of mesic affinities is now restricted to its highest elevations. The only reports on its plant composition were published at the end of the last century (Brandege 1891, 1892a, b, 1894, 1903).

The oak-pine woodland community that occurs in the upper elevations contains a high proportion of endemic taxa. Increasing human settlement in the vicinity has resulted in destructive use of this natural resource, and thus the plant community may be at risk of losing its natural balance.

#### STUDY AREA

*Topography.* The mountains of the Cape Region extend in a south-north direction, from 23°00' to 23°35'N lat. The range is crossed by the Tropic of Cancer. About 500 square km of these mountains are estimated to be above 1000 m elevation with the highest peak at 2200 m (El Picacho). The Sierra de la Laguna is located in the northern part of the Cape Region mountains. It includes five major canyons (Fig. 1), having an estimated surface of about 100 square km.

*Geology and soils.* The Sierra de la Laguna is composed totally of massive intrusive rocks, granites and syenites for the most part. It is an extension of a great batholith of Upper Jurassic or Lower Cretaceous age, which underlies most of the peninsula and presumably also parts of the Gulf of California (Beal 1948; Durham and Allison 1960). Most of these rocks are moderately coarse-grained and subject to rapid disintegration. The soils are sandy, with a thin layer of litter; the content of loam and clay is low. On slopes, foothills, and alluvial plains there are no differentiated soil layers. The soils are classified as Regosols (FAO-UNESCO system modified by Mexican government; Secretaría de Programación y Presupuesto 1981a). At the bottom of brooks and canyons some permanent pools occur on the hard rock bed. The courses of the canyons are a direct consequence of active erosion along their escarpments (Hammond 1954; López Ramos 1973). The eastern face of the Sierra is more precipitous than the western slopes. Similar patterns are present also



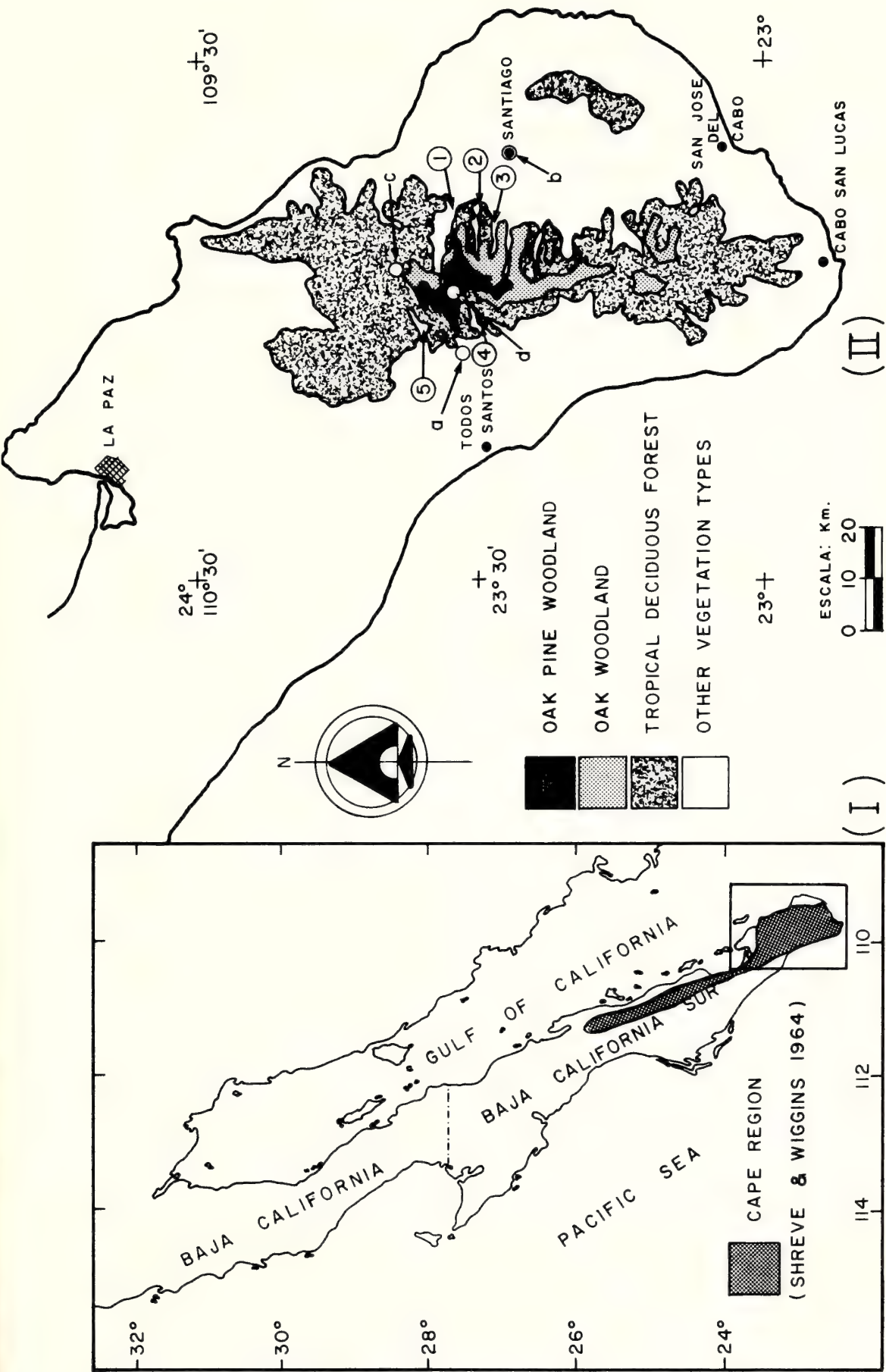


FIG. 1. Study area location. I. Position in Baja California Peninsula and Cape Region. II. Ubication of the Sierra de la Laguna, conformed by five major canyons: 1) San Jorge, 2) La Zorra, 3) San Jorge, and 5) Las Pilitas (Santa Inés). Vegetation types in the mountainous area are indicated by shading. Climatic stations: a. Santa Gertrudis, b. Santiago, c. San Bartolo, and d. La Laguna (see also Fig. 2).



in the Sierra de la Giganta and other ranges much further to the north, such as Sierra San Pedro Mártir, Sierra Juárez, and several others in California, USA.

*Climate.* Foothills and adjacent low areas have a warm climate; at higher elevations it is cooler, and light frosts occur during winter nights. Figure 2 shows yearly temperature and precipitation data obtained by García (1973) at one location at 1620 m and three sites at lower elevations (350–368 m). Climate in the summits, C(w1), is temperate, subhumid, with the main rains in summer, but some also in winter. At middle and low elevations occur BSo and BW types, respectively; the first (BSo) is semiarid, with rains mainly in the summer but scattered through the year; the second (BW) refers to a very dry and warm climate, with rains occurring mainly in the summer. Generally there is low precipitation in winter, but during the summer months rains occur as thunderstorms caused by cyclonic perturbations originating in the Pacific Ocean. Late winter to early summer are usually the driest seasons.

*Land use.* The high elevations of the mountains receive the most precipitation in an ample geographical surface (Fig. 2). These regions supply the aquifers that provide for many ranches, urban and suburban populations, and some small agricultural areas in one of the most arid regions of North America. Rural and urban populations as well as tourism around the area of Sierra de la Laguna are increasing rapidly. Recent population estimates derived from census data indicate approximately 250,000 inhabitants in the region. This population demands water to satisfy its primary needs; it is obtained totally from underground aquifers by pumping. The Sierra and its foothills support several human activities without efficient control; these include hunting, gathering of firewood or harvesting of trees, and both intensive and extensive livestock breeding.

For these reasons, it is necessary that simultaneously with the investigations of the flora and vegetation of the Sierra de la Laguna, studies must be made of its ecological aspects, both basic and applied (Halffter 1984). International (Man and Biosphere Program, MAB-UNESCO) and Mexican institutions and organizations have realized the importance of ecological preservation of the Sierra in order to protect the area from the destructive human activities noted above.

#### PLANT COMMUNITIES AND ASSOCIATIONS

Vegetation in the Sierra de la Laguna and adjacent areas is here organized into four plant communities. The nearly level alluvial lands and valleys with scattered low hills that surround the mountain body contain a “desert scrub” that, following modern Mexican sys-



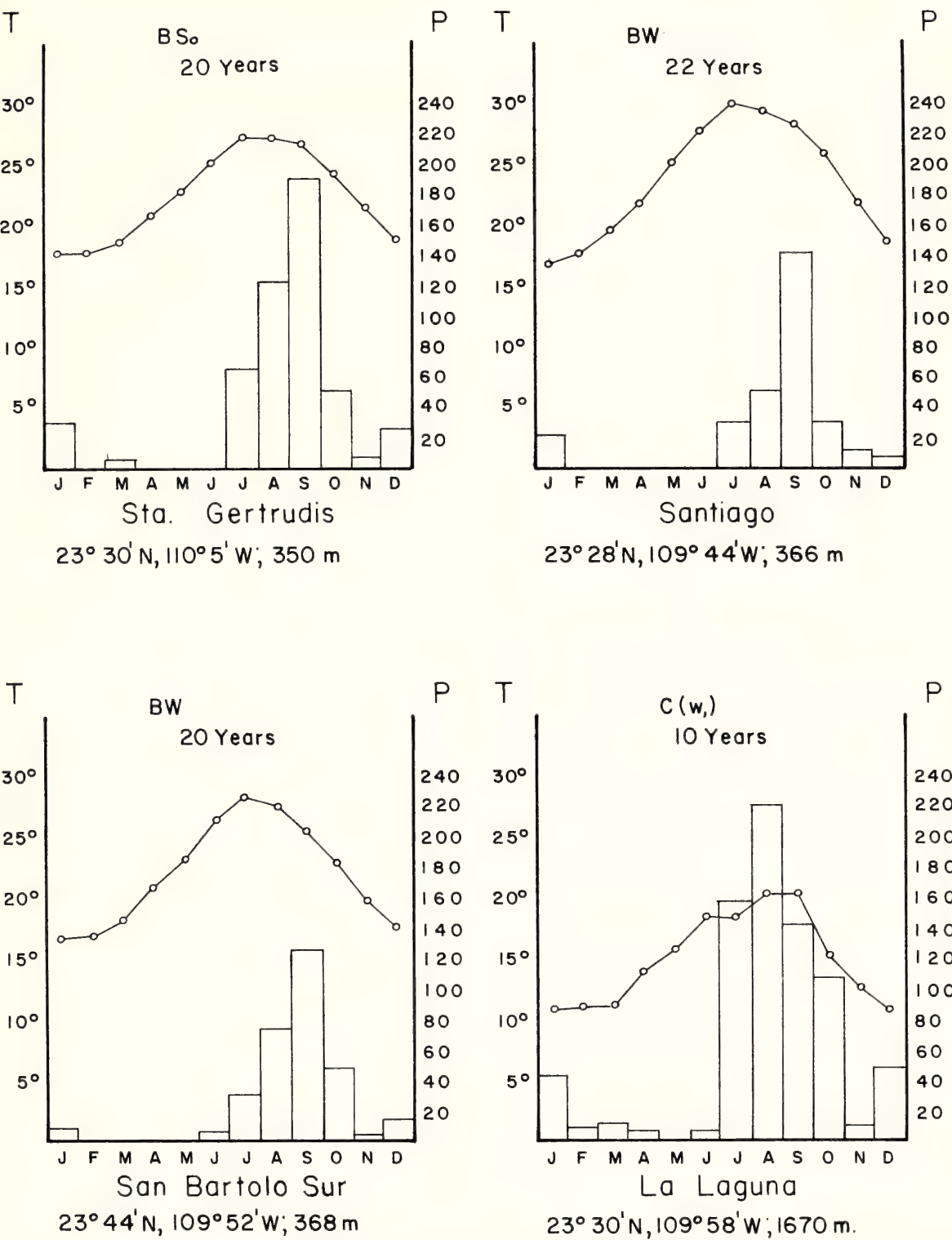


FIG. 2. Annual temperature (°C, connected circles) and rainfall precipitation (mm, histogram) in three localities at base of the Sierra de la Laguna, and a high elevation location on the same sierra. Koeppen climatic general formulas are indicated in each site; Bs relates a semiarid and hot climate, BW is very arid and warm, and C(cw) is a temperate and sub-humid one (see also Fig. 1).

tems (SPP–DGGTN 1981b), is designated as a “matorral sarcocaulle” (sarcocaullescent scrub). The pediplains with prominent hills and canyons from 400 to 1000 m elevation support a vegetation called “selva baja caducifolia” (low deciduous forest). The middle eleva-



TABLE 1. SOME DASONOMYCAL CHARACTERISTICS OF THE TREE STRATUM ON A SLOPE (20 DEGREES OF STEEPNESS) IN THE SIERRA DE LA LAGUNA OAK-PINE WOODLAND IN A 3000-SQUARE-M PLOT AT 1700 M.

| Species                                     | Number of individuals | Cover (square m) | Average height (m) |
|---|-----------------------|------------------|--------------------|
| <i>Quercus devia</i>                        | 68                    | 24.1             | 11.5               |
| <i>Arbutus peninsularis</i>                 | 61                    | 21.3             | 6.8                |
| <i>Pinus cembroides</i> var. <i>lagunae</i> | 45                    | 7.6              | 6.9                |
| <i>Nolina beldingii</i>                     | 14                    | 2.5              | 3.3                |
| <i>Prunus serotina</i> subsp. <i>virens</i> | 2                     | 7.4              | 6.4                |

tions (1000–1500 m) are covered by an oak woodland, and the upper elevations (1500–2200 m) by an oak-pine woodland.

1) *Oak-pine woodland*. This community can be divided into four types of associations or habitats, according to vegetative composition and physiognomy. For purposes of this study these are termed: “valleys”, “stream bottoms”, “true woodland”, and “open areas”.

The dominant species in the oak-pine woodland are *Pinus cembroides* var. *lagunae* (“piño piñonero), *Quercus devia* (“encino negro”), *Arbutus peninsularis* (“madroño”), and *Nolina beldingii* (“sotol”). Their relative densities vary within the different habitats. Table 1 illustrates the composition of the higher stratum of this woodland; the data were taken from “true woodland” habitat.

*Valleys*. These are open sunny areas in which both annual and short-lived perennial herbs are dominant. These areas are scattered through the Sierra. The largest, known as “La Laguna” (to which this range owes its name), is located at 1820 m (although another publication fixes it at 1620 m), and is crossed by permanent streams derived from the nearby mountain peaks. It is a flat-bottomed basin of almost 2 square km in surface. It is possible that in the recent past, La Laguna was a marsh, rather than a lagoon (Nelson 1921); a palynological study might provide important information on its natural history. An association of pinyon pine occurs at the valley margins, and it is here that the pines exhibit their maximum vigor. Two microenvironments can be distinguished in this habitat: a) streams and banks, and b) meadows. Some species typical of this association are listed below.

| Streams and banks            | Meadows                     |
|------------------------------|-----------------------------|
| <i>Bacopa monieri</i>        | <i>Bidens nudata</i>        |
| <i>Hydrocotyle umbellata</i> | <i>Centaurium nudicaule</i> |
| <i>Mimulus guttatus</i>      | <i>Cosmos parviflorus</i>   |



*Nasturtium officinale*  
*Polygonum punctatum*  
*Potamogeton foliosus*  
*Tinantia modesta*

*Lepechinia hastata*  
*Lycurus phleoides*  
*Oxalis albicans*  
*Tagetes micrantha*

*Stream bottoms.* These areas are characterized by high soil moisture. Trees and shrubs here are generally taller than elsewhere in the range. These include *Quercus rugosa* ("encino blanco"), *Q. arizonica*, *Ilex brandegeana* ("manzanita"), *I. californica* ("palo extraño"), and *Prunus serotina* subsp. *virens* ("cerezo"), all of which also occur in the Sierra Madre Occidental in mainland Mexico. In addition there are species such as *Heteromeles arbutifolia* ("toyón"), whose main distribution is in California chaparral. Species of this association include:

*Adiantum capillus-veneris*  
*Arethusa rosea*  
*Cyperus pallidicolor*  
*Epipactis giganteum*  
*Equisetum hyemale*  
     var. *affine*  
*Polypodium guttatum*

*Rhus radicans*  
*Ribes brandegeei*  
*Rubus scolocaulon*  
*Styrax argenteus*  
*Thelypteris puberula*  
*Tripsacum lanceolatum*

*True oak-pine woodland.* This is the most common habitat along the Sierra. It contains many annuals, short-lived perennials, and woody species that vary in relative density from one site to another. This can be attributed to such features as steepness of the slope, exposure to light, elevation, and successional stage of the area. It is opportune to mention that this plant association is constantly disturbed by fire; there are practically no areas of forest without recent evidence of fire from both natural and human causes. Selected shrubby and woody species include:

*Calliandra peninsularis*  
*Helianthemum glomeratum*  
*Helianthus similis*  
*Heterotoma aurita*  
*Hypericum peninsularis*

*Lepechinia hastata*  
*Mimosa xantii*  
*Perezia pinetorum*  
*Rumfordia connata*  
*Verbesina pustulata*

Some short-lived herbs are:

*Arracacia brandegeei*  
*Desmodium prostratum*  
*Gibasis heterophylla*  
*Gnaphalium bicolor*  
*Malaxis unifolia*

*Linanthus nuttalli* subsp.  
     *nuttalli*  
*Oenothera tetraptera*  
*Stachys coccinea*  
*Tagetes lacera*  
*Verbena carolina*



*Open areas.* These widely distributed areas are of two types; one consists of an early successional stage induced by fire and contains such species as *Muhlenbergia emersleyi*, *Rhynchelytrum repens*, *Bernardia lagunensis*, *Dodonaea viscosa*, and *Tephrosia cana*. Other open areas occur on prominent rocks, with high exposure to sun and thin soil. These areas contain such species as *Morangaya pensilis*, *Mammillaria petrophilla*, *Hechtia montana*, *Daphnopsis* [undescribed sp.], *Myrtillocactus cochal*, *Dudleya nubigena*, *Agave promontorii*, and *Russelia retrorsa*.

2) *Oak woodland.* The area occupied by this community is very precipitous, with slopes ranging from 30° to 40°. The strata consist of trees, low shrubs, and both annual and perennial herbs. Trees are scattered. *Quercus tuberculata* ("encino roble") characterizes the entire woodland. Also, it is common to find some species from the tropical deciduous forest and other communities of the lowlands.

Low shrubs usually are scattered, but grow more densely in some areas. Common species are *Mimosa xantii*, *Arracacia brandegeei*, *Dodonaea viscosa*, *Tephrosia cana*, *Bernardia lagunensis*. Herbs are typically represented by such bunchgrasses as *Muhlenbergia emersleyi*, *Heteropogon contortus*, and *Schizachyrium sanguineum* var. *brevipedicellatum*, and small herbs such as *Tagetes subulata*, *Crotalaria saggitalis*, *Heterosperma xantii*, and *Zornia reticulata*. Vines such as *Phaseolus filiformis* and *Quamoclit coccinea* var. *coccinea* are abundant after the rainy season.

Finally, a local riparian plant association occupies the bottom of the brooks and canyons, descending with the streams until these disappear at elevations of 300 to 500 m. At middle elevations this association is characterized by *Populus brandegeei* var. *glabra* ("güeribo"), *Salix lasiolepis* ("sauce"), and the fan palms *Erythea brandegeei* and *Washingtonia robusta*.

## FLORA

A total of 228 taxa of vascular plants have been identified from this region to date; another ten taxa await identification. These represent 66 families and 172 genera. Excluding such large families as Compositae, Gramineae, and Leguminosae, these have a genus to species ratio of about 1:1.5. Thirty-seven species and infraspecific taxa are considered to be endemic (approximately 17%). The area contains two endemic genera: *Faxonia* (Compositae) and *Morangaya* (Cactaceae). The proportion of endemic species is moderate as compared with the closest biotic provinces (the Californian with about 48% and the Sonoran Desert with about 23%), but these are hundreds of times greater in total surface (Wiggins 1980).

Table 2 shows the frequency of life forms in the sierra. "Perennial Herbs" includes such short-lived herbs as root perennials. "Hy-



TABLE 2. LIFE FORMS ADOPTED IN THIS WORK FOR THE VASCULAR PLANTS OF THE SIERRA DE LA LAGUNA (see text and annotated catalog).

| Life form               | Symbol in the catalog | Number of species |
|-------------------------|-----------------------|-------------------|
| Trees                   | Ar                    | 16                |
| Shrubs and subshrubs    | Ab                    | 24                |
| Perennial herbs         | Hp                    | 97                |
| Annuals                 | An                    | 47                |
| Hydrophytes             | Hf                    | 30                |
| Macrosucculents (cacti) | Sm                    | 5                 |
| Microsucculents         | Si                    | 3                 |
| Annual vines            | Th                    | 3                 |
| Perennial vines         | Tl                    | 2                 |
| Parasites               | Pa                    | 1                 |
| Total                   |                       | 228               |

drophytes” are all those herbs which grow in or close to streams. Succulents are divided into “Macro” and “Micro” (e.g., *Opuntia* vs. *Mammillaria*, respectively).

*Rare plants.* Almost a century ago T. S. Brandegee described *Faxonia pusilla* from a single plant; it has not been collected since, and may well be extinct. *Pectis uniaristata*, *Muhlenbergia wolfii*, and *M. ciliata*, all collected by Brandegee, have not been found by the authors, and may no longer occur in the Sierra de la Laguna. *Eriogonum inflatum* var. *deflatum* and *Arenaria lanuginosa* subsp. *saxosa* were reported by Wiggins (1980) but we have not collected them. Specimens of *Ilex californica* are very scarce; only a dozen living trees are known.

Other species with very restricted localities and relatively few individuals are *Aralia scopulorum*, *Conopholis mexicana*, *Ilex brandegeana*, *Myrtillocactus cochal*, *Polygala apopetala*, *Quercus arizonica*, *Q. oblongifolia*, and *Q. reticulata*.

*Methods.* Between 1980 and 1987 28 visits were made to the area in all four seasons. Almost a thousand voucher specimens were prepared and are housed in the herbarium of Centro de Investigaciones Biológicas de Baja California Sur (CIB). Nomenclature follows mainly that of Wiggins (1980). Most of the determinations were checked by comparison with specimens at CAS and UC. Current regional authorities are followed wherever possible.

*Annotated catalog.* Each entry includes information on life form (cf. Table 2), habitat, occurrence, flowering phenology, and common name. Endemic species are marked with an asterisk (\*). In some cases, synonyms are included. The catalog is placed as Appendix 1 at the end of the paper.



TABLE 3. COMPARISON OF PLANT FAMILIES AND NUMBER OF SPECIES BETWEEN BRANDEGEE (1891) AND PRESENT WORK FOR THE SIERRA DE LA LAGUNA MOUNTAINS. Family synonyms are included where names used for taxa differ.

| Brandegee (1891)      |    | León and Domínguez |    |
|-----------------------|----|--------------------|----|
| Ferns and fern allies |    |                    |    |
| Filices               | 16 | Equisetaceae       | 1  |
|                       |    | Polypodiaceae      | 13 |
|                       |    | Schizaeaceae       | 1  |
|                       |    | Selaginellaceae    | 2  |
| Gymnospermae          |    |                    |    |
| Coniferae             | 1  | Pinaceae           | 1  |
| Angiospermae          |    |                    |    |
| Dicotyledones         |    |                    |    |
| Acanthaceae           | 1  |                    | 1  |
| Amaranthaceae         | 1  |                    | 0  |
| Anacardiaceae         | 2  |                    | 3  |
| Umbelliferae          | 1  |                    | 2  |
| Aquifoliaceae         | 0  |                    | 2  |
| Begoniaceae           | 1  |                    | 0  |
| Cruciferae            | 3  |                    | 2  |
| Cactaceae             | 1  | Campanulaceae      | 4  |
| Lobeliaceae           | 2  |                    | 2  |
| Caryophyllaceae       | 6  |                    | 5  |
| Chenopodiaceae        | 0  |                    | 1  |
| Cistaceae             | 2  |                    | 1  |
| Cornaceae             | 1  |                    | 0  |
| Compositae            | 21 |                    | 26 |
| Convolvulaceae        | 1  |                    | 2  |
| Crassulaceae          | 0  |                    | 2  |
| Cucurbitaceae         | 1  |                    | 1  |
| Cupuliferae           | 2  | Fagaceae           | 5  |
| Ericaceae             | 1  |                    | 1  |
| Euphorbiaceae         | 0  |                    | 6  |
| Garryaceae            | 0  |                    | 1  |
| Gentianaceae          | 2  |                    | 1  |
| Geraniaceae           | 2  |                    | 2  |
| Grossulariaceae       | 0  |                    | 1  |
| Hypericaceae          | 2  |                    | 2  |
| Labiatae              | 4  |                    | 5  |
| Leguminosae           | 14 |                    | 14 |
| Loganiaceae           | 0  |                    | 1  |
| Lythraceae            | 1  |                    | 0  |
| Malvaceae             | 1  |                    | 0  |
| Nyctaginaceae         | 1  |                    | 1  |
| Onagraceae            | 3  |                    | 5  |
| Orobanchaceae         | 1  |                    | 1  |
| Oxalidaceae           | 0  |                    | 2  |
| Phytolaccaceae        | 0  |                    | 1  |
| Piperaceae            | 1  |                    | 1  |
| Plantaginaceae        | 2  |                    | 2  |
| Podostemonaceae       | 0  |                    | 1  |
| Polygonaceae          | 1  |                    | 2  |



TABLE 3. CONTINUED.

| Brandegee (1891) |     | León and Domínguez |     |
|------------------|-----|--------------------|-----|
| Polygalaceae     | 2   |                    | 1   |
| Primulaceae      | 2   |                    | 1   |
| Ranunculaceae    | 2   |                    | 3   |
| Rosaceae         | 5   |                    | 5   |
| Rubiaceae        | 2   |                    | 8   |
| Salicaceae       | 2   |                    | 2   |
| Sapindaceae      | 1   |                    | 1   |
| Saxifragaceae    | 1   |                    | 0   |
| Scrophulariaceae | 1   |                    | 5   |
| Solanaceae       | 1   |                    | 1   |
| Styracaceae      | 0   |                    | 1   |
| Thymelaeaceae    | 0   |                    | 1   |
| Valerianaceae    | 1   |                    | 1   |
| Verbenaceae      | 0   |                    | 1   |
| Vitaceae         | 1   |                    | 1   |
| Monocotyledones  |     |                    |     |
| Agavaceae        | 0   |                    | 3   |
| Liliaceae        | 1   | Amaryllidaceae     | 1   |
| Palmaceae        | 1   | Palmae             | 2   |
| Bromeliaceae     | 0   |                    | 1   |
| Commelinaceae    | 0   |                    | 5   |
| Cyperaceae       | 2   |                    | 9   |
| Iridaceae        | 1   |                    | 1   |
| Juncaceae        | 1   |                    | 1   |
| Lemnaceae        | 1   |                    | 1   |
| Naiadaceae       | 1   |                    | 0   |
| Orchidaceae      | 9   |                    | 9   |
| Gramineae        | 8   |                    | 33  |
| Potamogetonaceae | 0   |                    | 2   |
|                  | 146 |                    | 228 |

DISCUSSION

Wiggins' flora (1980) reportedly lists the vascular plants known from the entire Baja California Peninsula. The flora integrates data from previous works such as Shreve and Wiggins (1964), Munz (1968), and Standley (1920–1924). The Cape Region, in particular the montane areas, has an incomplete representation in Wiggins' flora. About 25% of the plants listed in our catalog were omitted from Wiggins' flora, or, in some cases, reported from other areas of the peninsula but not from the Sierra de la Laguna region.

The vegetation of the Cape Region, as a whole, has been stated to have many tropical features (Brandegee 1891; Shreve 1937; Wiggins 1960, 1980; Rzedowski 1978), but the Sierra de la Laguna woodland is distinct in its life forms and species composition. Most of its flora is considered to be relictual (Axelrod 1950, 1958). Further investigations must be carried out to characterize it phytogeographically.



Brandeggee (1892a) initially reported 146 species of vascular plants from the "high elevations" of the Cape Region, with additional taxa reported in later works (Brandeggee 1892b, 1894, 1903). At present, it is difficult to identify the limits of Brandeggee's territory, but it is reasonable to suggest that it corresponds with the area defined here. Our enumeration lists 227 taxa, with an additional 10 taxa still awaiting identification. Brandeggee reported 7 families which we have not yet recorded, and we list 16 families which he did not report (Table 3). This would imply that Brandeggee's initial work was incomplete, but it is also possible that after almost 100 years the community has been enriched by various introduced species. Both assumptions may be true (Gilmartin and Neighbours 1978).

The Mexican "Selva Baja Caducifolia" (Low Deciduous Forest; Miranda and Hernández X. 1963), or "Bosque Tropical Caducifolio" (Tropical Deciduous Forest; Rzedowski 1978) is a relatively large plant community which is located in the foothills and nearby areas of the Cape Region mountains (Fig. 1). It is undoubtedly one of the richest plant communities of the entire peninsula. Shreve (1937) noted the scientific importance of having reliable knowledge of this community; it is a transition between the xeric (Sonoran Desert) and the intertropical in the Mexican Pacific coast. The tropical communities of the Cape Region, as well as the woodlands described above, evolved under isolated conditions from the nearest areas of similar climate. The first plant communities must be studied intensively in the future.

#### ACKNOWLEDGMENTS

We are grateful to Annetta M. Carter, Amy J. Gilmartin, Lincoln Constance, and S. L. Hatch for their highly esteemed collaboration. We acknowledge also Arturo Gómez-Pompa for his financial support that enabled us to check part of our material in the DS-CAS and UC herbaria. This research was supported by a grant from CONACYT-SPP, México.

#### LITERATURE CITED

- AXELROD, D. I. 1950. Classification of the Madro-Tertiary flora. Publ. Carnegie Inst. Wash. 590:1-22.  
———. 1958. Evolution of the Madro-Tertiary geoflora. Bot. Rev. (Crawfordsville) 24:434-509.  
BEAL, C. H. 1948. Reconnaissance of the geology and oil possibilities of Baja California, Mexico. Mem. Geol. Soc. Amer. 33.  
BRANDEGEE, T. S. 1891. Flora of the Cape District of Baja California. Proc. Cal. Acad. Sci., ser. 2, 3:8-182.  
———. 1892a. Distribution of the flora of the Cape Region of Baja California. Zoe 3:223-231.  
———. 1892b. Additions to the flora of the Cape Region of Baja California. Proc. Cal. Acad. Sci., ser. 2, 3:218-227.  
———. 1894. Additions to the flora of the Cape Region of Baja California. Zoe 4: 108-131.



- . 1903. Notes and new species of Lower California plants. *Zoe* 5:155–173.
- BRYANT, W. E. 1891. The Cape Region of Baja California. *Zoe* 2:185–201.
- DURHAM, J. W. and E. C. ALLISON. 1960. The geologic history of Baja California and its marine fauna. *Syst. Zool.* 9:47–91.
- GARCÍA, E. 1973. Modificaciones al sistema de clasificación de Koppen, 2nd ed. Inst. Geogr. Univ. Nal. Aut. Mex., Mexico, D.F. 246 pp.
- GILMARTIN, A. J. and M. L. NEIGHBOURS. 1978. Flora of the Cape Region of Baja California Sur. Res. Rep. Natl. Geogr. Soc., 1969 Projects, pp. 219–225.
- GOULD, F. W. and R. MORAN. 1981. The grasses of Baja California, Mexico. *Mem. San Diego Soc. Nat. Hist.* 12:1–140.
- HALFFTER, G. 1984. Biosphere reserves: the conservation of nature for man. *Inst. Ecol. Mex. Acta Zool. Mex.* 5:31–50.
- HAMMOND, E. H. 1954. A geomorphic study of the Cape Region of Baja California. Univ. California Press, Berkeley. 98 pp.
- JOHNSON, B. H. 1958. The botany of the California Academy of Sciences Expedition to Baja California in 1941. *Wasmann J. Biol.* 16:217–315.
- LÓPEZ-RAMOS, E. 1973. Carta geológica del territorio de Baja California. Inst. Geología, Univ. Nal. Aut. Mex.
- MIRANDA, F. and E. HERNÁNDEZ X. 1963. Los tipos de vegetación de México y su clasificación. *Bol. Soc. Bot. Mex.* 28:29–179.
- MUNZ, P. A. 1968. A California flora and supplement. Univ. California Press, Berkeley. 1681 + 224 pp.
- NELSON, E. W. 1921. Baja California and its natural resources. *Mem. Natl. Acad. Sci.* 16:1–194.
- RZEDOWSKI, J. 1978. Vegetación de México. Editorial Limusa, México, D.F. 432 pp.
- SECRETARÍA DE PROGRAMACION Y PRESUPUESTO. 1981a. Dirección general de geografía del territorio nacional, México. Carta geológica 1:100,000.
- . 1981b. Dirección general de geografía del territorio nacional, México. Carta de uso del suelo y vegetación 1:100,000.
- SHREVE, F. 1937. Vegetation of the Cape Region of Baja California. *Madroño* 4: 105–113.
- and I. L. WIGGINS. 1964. Vegetation and flora of the Sonoran Desert, 2 vols. Stanford Univ. Press, Stanford, CA.
- STANDLEY, P. C. 1920–1924. Trees and shrubs of Mexico. *Contr. U.S. Natl. Herb.* 23:1–1721.
- WIGGINS, I. L. 1960. The origin and relationships of the land flora. *In* The biogeography of Baja California and adjacent seas. *Syst. Zool.* 9:148–165.
- . 1980. Flora of Baja California. Stanford Univ. Press, Stanford, CA. 1025 pp.

(Received 9 Apr 1987; resubmitted 17 Feb 1988; revision accepted 9 Nov 1988.)

#### APPENDIX 1

#### Ferns and Allies

#### Equisetaceae

*Equisetum hyemale* L. var. *affine* (Engelm.) A. A. Eaton. Hf; stream bottoms; locally abundant; Jan.

#### Polypodiaceae

*Adiantum capillus-veneris* L. Hf; stream bottoms; common under rocks; Sep–Dec.

*Asplenium blepharodes* D. Eaton. Hf; stream bottoms; common; Sep–Nov.

*Asplenium monanthes* L. Hf; stream bottoms; rare; Sep–Nov.



*Cheilanthes pyramidalis* Fée. Hf; stream bottoms; rare; Sep–Dec.

*Dryopteris patula* (Sw.) Underw. var. *rosii* C. Chr. Hf; stream bottoms; uncommon; Aug–Nov.

*Pellaea ternifolia* (Cav.) Link var. *ternifolia*. Hp; open areas, around boulders; common; Aug–Oct; “helecho peyote”.

*Pityrogramma triangularis* (Kaulf.) Maxon var. *maxonii* Weath. Hp; stream bottoms, among rocks; uncommon; Aug–Nov.

*Pleopeltis polylepis* (Roem. & Kunze) Moore. Hp; stream bottoms; locally abundant; Aug–Nov.

*Polypodium guttatum* Maxon. Hf; stream bottoms; common; Sep–Dec.

*Polypodium lanceolatum* L. Hf; stream bottoms, among rocks; common; Sep–Nov.

*Pteridium aquilinum* (L.) Kuhn var. *lanuginosum* (Borg.) Fern. Hf; stream bottoms; common; Aug–Jan.

*Thelypteris puberula* (Baker) C. Morton var. *sonoriensis* A. R. Smith. Hf; stream bottoms, oak woodland; locally abundant; Sep–Jan.

*Woodsia plummerae* Lemmon. Hp; stream bottoms; locally abundant; Sep–Oct.

#### Selaginellaceae

*Selaginella bigelovii* Underw. Hp; stream bottoms; locally abundant; Jul–Oct.

*Selaginella pallescens* (Presl) Spring. Hp; stream bottoms, oak woodland; locally abundant; Jul–Oct.

#### Schizaeaceae

*Anemia hirsuta* (L.) Sw. Hp; stream bottoms, oak woodland; rare; Oct.

#### Gymnospermae

##### Pinaceae

\**Pinus cembroides* Zucc. var. *lagunae* M. F. Robert. Ar; true woodland, stream bottoms, valley edges, open areas; common; May–Jun; “piño piñonero” (*P. lagunae* (Robert-Passini) M. F. Passini).

#### Angiospermae

##### Dicotyledones

##### Acanthaceae

*Dicliptera resupinata* (M. Vahl) Juss. Ab; open areas, oak woodland, among rocks; rare; Oct–Mar.

#### Anacardiaceae

*Rhus laurina* Nutt. Ab; stream bottoms; scattered locations; Apr–Jul; “lentil”.

*Rhus schiediana* Schlecht subsp. *tepetate* (Standley & F. Barkley) D. A. Young. Ab; stream bottoms; more gregarious than *R. laurina*; Jul–Aug (*R. tepetate* Standley & F. Barkley).

*Rhus radicans* L. var. *divaricata* (E. Greene) Fern. Tl; stream bottoms, on rocks and trees; occasional populations; May–Jun (often treated as *Toxicodendron radicans* (L.) Kuntze).

#### Aquifoliaceae

*Ilex brandegeana* Loes. Ar; stream bottoms; scattered small populations; May–Jun; “manzanita” (*I. triflora* Brandegeae).

\**Ilex californica* Brandegeae. Ar; stream bottoms; only a few specimens known; Apr–May; “palo extraño” (*I. toluhana* Hemsl.).



## Cactaceae

- \**Mammillaria petrophilla* K. Brandegee. Si; open areas; occasional populations on crevices; Jan–May.  
 \**Morangaya pensilis* (K. Brandegee) Rowley. Sm; open areas; small populations found hanging on rocks; Mar ?; “clavellina”.  
*Myrtillocactus cochal* (Orc.) Britton & Rose. Sm; open areas; found only at the Picacho Peak; May–Jun.  
 \**Opuntia lagunae* K. Brandegee. Sm; valleys; common, bordering meadows; May–Jun.

## Campanulaceae

- Heterotoma aurita* Brandegee. An; stream bottoms, true woodland; common; Dec–May.  
*Lobelia laxiflora* Kunth var. *angustifolia* A. DC. Hp; stream bottoms; occasional in stream banks; Jan–Jul.

## Caryophyllaceae

- Arenaria lanuginosa* Rohrb. subsp. *saxosa* (A. Gray) Maguire. Hp; valleys; rare; Jul–Sep; no voucher.  
*Drymaria glandulosa* Presl. An; stream bottoms; occasional; Aug–Feb.  
*Paronychia mexicana* Hemsl. subsp. *monandra* (Brandegee) Chaudhri. Hp; valleys; occasional; Aug–Nov.  
*Silene laciniata* Cav. subsp. *brandegeei* C. Hitch. & Maguire. Hp; stream bottoms; occasional; Sep–Nov.  
*Stellaria nitens* Nutt. in Torrey & A. Gray. An; stream bottoms; small populations; Feb–Apr.

## Chenopodiaceae

- Chenopodium ambrosioides* L. An; stream bottoms; rare; any month; “epazote”; introduced.

## Cistaceae

- Helianthemum glomeratum* Lagasca ex DC. Hp; valleys, true woodland; open areas; stream bottoms; common; any month.

## Compositae (Asteraceae)

- Bidens aurea* (Dryander) Sherff. An; valleys, oak woodland; common, sandy stream banks; Sep–Oct; “aceitilla”.  
*Bidens bigelovii* A. Gray var. *pueblensis* Sherff. An; valleys; common; Sep–Oct; “aceitilla”.  
 \**Bidens nudata* Brandegee. Hp; open areas, oak woodland; uncommon; Aug–Oct.  
*Brickellia peninsularis* Brandegee. Hp; open areas, oak woodland; rare; Nov–Feb.  
*Carminatia tenuiflora* DC. An; open areas, oak woodland; common; Sep–Nov.  
*Conyza bonariensis* (L.) Cronq. An; valleys; uncommon in sandy stream banks; Oct–Dec.  
*Conyza canadensis* (L.) Cronq. An; valleys; uncommon in meadows; Oct–Jan.  
*Conyza coulteri* A. Gray. An; valleys; rare; Aug–Oct.  
*Cosmos parviflorus* (Jacq.) Pers. An; valleys; common in meadows and stream banks; Sep–Oct.  
 \**Eupatorium purpusii* Brandegee var. *monticulum* Brandegee. Hp; true woodland; uncommon; Feb–Apr (*Ageratina purpusii* (Brandegee) R. King & H. Robinson).  
 \**Faxonia pusilla* Brandegee. An; valleys; collected only one time a century ago; Sep?; no voucher.



- Galinsoga ciliata* (Raf.) S. F. Blake. An; valleys; occasional, sandy stream banks; Sep–Nov.
- Gnaphalium bicolor* Bioletti. Hp; valleys, true woodland; widespread; Mar–Aug.
- Gnaphalium purpureum* L. An; valleys, stream bottoms; occasional; Apr–Sep.
- \**Helianthus similis* (Brandeggee) S. F. Blake. Ab; stream bottom, true woodland, open areas; widespread; Oct–Dec; “tacote de la Sierra”.
- Heterosperma xantii* A. Gray. Hp; open areas, oak woodland; common on disturbed soil; Mar–Sep.
- Hieracium fendleri* Schultz-Bip. Hp; stream bottoms; uncommon; Nov–Feb.
- \**Malacothrix carterae* W. Davis. Hp; stream bottoms; uncommon; Jan–Feb.
- Pectis uniaristata* DC. var. *uniaristata*. An; collected by Brandeggee almost a century ago, there is not additional information; no voucher.
- \**Perezia pinetorum* Brandeggee. Hp; true woodland, stream bottoms; occasional; Oct–Dec.
- Porophyllum ochroleucum* Rydb. Hp; true woodland, open areas, occasional in oak woodland; uncommon; Oct–Jan; “hierba del venado”.
- \**Rumfordia connata* Brandeggee. Hp; true woodland; uncommon; Jun–Aug; “tacote ceroso”.
- \**Tagetes lacera* Brandeggee. Hp; true woodland, stream bottoms; common; Sep–Oct; “cempasúchil”.
- Tagetes micrantha* Cav. An; valleys, open areas; abundant; Sep–Oct; “anisillo”.
- Tagetes subulata* Cerv. An; oak woodland; abundant; Oct.
- \**Verbesina pustulata* M. E. Jones. Hp; true woodland; uncommon; Aug–Oct; “tacote chino”.

#### Convolvulaceae

- Ipomoea leptotoma* Torr. Hp; oak woodland; locally abundant; Sep–Oct.
- Quamoclit coccinea* (L.) Moench var. *coccinea*. Th; oak woodland, mainly, rare in the valleys; Sep–Oct.

#### Crassulaceae

- Dudleya nubigena* (Brandeggee) Britton & Rose. Si; open areas; uncommon; Sep–Nov.
- Dudleya rigida* Rose. Si; open areas; less common than the preceding species; Oct?; no voucher.

#### Cruciferae (Brassicaceae)

- Lepidium virginicum* L. An; valleys, stream banks; common; May–Sep.
- Nasturtium officinale* R. Br. Hf; valleys, stream currents; abundant; Mar–Jul (*Rorippa nasturtium-aquaticum* (L.) Schinz. & Thell.).

#### Cucurbitaceae

- \**Cyclanthera testudinea* Brandeggee. Th; true woodland, stream bottoms; occasional; Sep; (*Cyclanthera tamnoides* Cogn.).

#### Ericaceae

- \**Arbutus peninsularis* Rose & Goldman. Ar; widespread in all oak-pine woodland habitats; Apr–May; “madroño”.

#### Euphorbiaceae

- Acalypha comonduana* Millsp. Ab; true woodland, open areas; occasional on rocky hillsides; Apr–Jul.
- \**Bernardia lagunensis* (M. E. Jones) Wheeler. Ab; other open areas, oak woodland; common; Oct–Nov.



\**Croton boregensis* M. E. Jones. Ab; oak woodland; occasional, more common in lower communities; Aug–Oct.

*Croton magdalenae* Millsp. Ab; oak woodland; rare; Jul–Aug.

\**Euphorbia lagunensis* Huft. An; valleys, true woodland; uncommon; Sep–Oct.

*Phyllanthus acuminatus* Vahl. Ab; true woodland, stream bottoms, oak woodland; occasional; Oct–Jan.

#### Fagaceae

*Quercus arizonica* Sarg. Ar; stream bottoms; small population found; Apr–May?.

\**Quercus devia* Goldman. Ar; stream bottoms; true woodland; abundant; Apr–Jun; “encino negro”.

*Quercus rugosa* Née. Ar; stream bottoms; small population found; Apr–May; “encino blanco” (*Q. reticulata* Humb. & Bonpl.).

*Quercus tuberculata* Liebm. Ar; stream bottoms and oak woodland; occasional and common, respectively; Mar–Apr; “encino roble”.

*Quercus oblongifolia* Torr. Ar; true woodland; found at two sites, small populations in oak woodland; Apr–May?; “encino laurel”.

#### Garryaceae

\**Garrya salicifolia* Eastw. Ab; stream bottoms; occasional; Sep–Nov; “yerba prieta”.

#### Gentianaceae

*Centaurium nudicaule* (Engelm.) Robinson. An; valleys; abundant; Mar–Apr.

#### Geraniaceae

*Geranium flaccidum* Small. Hp; stream bottoms; occasional; Sep–Oct.

*Geranium molle* L. An; valleys, stream bottoms; occasional on stream banks and grassy slopes; Feb–May.

#### Grossulariaceae

\**Ribes brandegeei* Eastw. Ab; stream bottoms; uncommon, small populations; Jan–Mar.

#### Guttiferae (Hypericaceae, Clusiaceae)

*Hypericum anagalloides* Cham. & Schldl. Hp; valleys, stream bottoms; uncommon, muddy habitats; Jan–Feb.

*Hypericum peninsulare* Eastw. Ab; valleys, true woodland; widespread; flowering any month.

#### Labiatae (Lamiaceae)

*Lepechinia hastata* (A. Gray) Epling. Hp; valleys, stream bottoms, true woodland; widespread; Aug–Feb; “chicura de la sierra”.

\**Monardella lagunensis* M. E. Jones. Hf; valleys, along stream currents; occasional; Sep.

*Prunella vulgaris* L. subsp. *lanceolata* (Barton) Hultén. An; valleys, true woodland; rare; Jul–Sep.

*Salvia similis* Brandege. Hp; open areas, oak woodland; rare; Sep–Feb.

*Stachys coccinea* Jacq. An; true woodland, stream bottoms, open areas; common; Oct–Jan.

#### Leguminosae (Fabaceae)

\**Astragalus francisquitensis* M. E. Jones var. *lagunensis* M. E. Jones. An; valleys, open areas, oak woodland; widespread; Dec–May.



- \**Calliandra peninsularis* Rose. Ab; true woodland, stream bottoms; common; Apr–Nov; “tabardillo de la sierra”.
- Crotalaria sagittalis* L. An; valleys, open areas, oak woodland; uncommon; Sep–Feb; “cascabelito”.
- Dalea divaricata* Benth. subsp. *anthonyi* (Brandeggee) Abrams. Hp; open areas, oak woodland; locally abundant Nov–Mar (*Marina divaricata* (Benth.) Barneby).
- Dalea trochilina* Brandeggee. Ab; stream bottoms; locally abundant; May–Jul (*Dalea seemannii* subsp. *trochilina* (Brandeggee) Wiggins).
- Desmodium mollicum* (Kunth.) DC. Hp; stream bottoms; found in a few sites; Sep.
- Desmodium procumbens* (Mill.) A. Hitchc. Hp; true woodland, stream bottoms, oak woodland; scattered locations; Aug–Sep.
- \**Desmodium prostratum* Brandeggee. Hp; true woodland, stream bottoms; common; Aug–Oct.
- \**Lupinus lagunensis* M. E. Jones. An; true woodland, stream bottoms, common; Dec–Feb.
- Mimosa xantii* A. Gray. Ab; true woodland, stream bottoms, open areas, oak woodland; common; Mar–Jul; “celosa”.
- Phaseolus filiformis* Benth. Th; open areas, oak woodland; common; Sep–Nov; “frijolillo”.
- Tephrosia cana* Brandeggee. Ab; open areas, oak woodland; occasional; Oct–Dec.
- Trifolium wormskjoldii* Lehm. Hf; valleys, stream currents; common; May–Aug; “trebol”.
- Zornia reticulata* Smith. Hp; open areas, oak woodland; widespread; Aug–Oct.

#### Loganiaceae

- Buddleja crotonoides* A. Gray. Ab; stream bottoms, oak woodland; uncommon; Mar–Apr; “lengua de buey”.

#### Nyctaginaceae

- Mirabilis jalapa* L. Hp; true woodland, open areas; abundant locally; Aug–Oct; “maravilla”.

#### Onagraceae

- Epilobium glaberrima* Barbey. Hf; valleys, stream bottoms; along stream currents; occasional; Jun–Aug.
- Lopezia clavata* Brandeggee. An; true woodland; rare; Sep–Oct.
- Oenothera laciniata* Hill subsp. *pubescens* (Willd.) Raven. Hp; bordering the valleys; common; Sep–Oct.
- Oenothera tetraptera* Cav. Hp; valleys, meadows; common; Sep–Oct.
- \**Oenothera* sp. (undescribed). Hp; valleys; rare; Sep.

#### Orobanchaceae

- Conopholis mexicana* A. Gray. Pa; stream bottoms; locally abundant; Sep–Oct.

#### Oxalidaceae

- Oxalis albicans* Kunth. Hp; valleys, true woodland; common; any month.
- Oxalis nudiflora* Mociño & Sessé. Hp; stream bottoms; uncommon; Aug–Nov.

#### Phytolaccaceae

- Phytolacca octandra* L. Hp; margin of valleys; rare (may be introduced from the lowlands); Aug–May.



## Piperaceae

*Peperomia umbilicata* Ruíz & Pavón. An; stream bottoms; locally abundant; Sep.

## Plantaginaceae

*Plantago hirtella* Kunth. var. *galleotiana* (Decné.) Pilger. Hp; valleys, stream bottoms, along stream banks, about seeps; locally abundant; Aug–Nov.

*Plantago linearis* Kunth. var. *mexicana* (Link) Pilger. Hp; valleys, grassy stream banks and meadows; Oct–Dec.

## Polemoniaceae

*Linanthus nuttalli* (A. Gray) E. Greene subsp. *nuttalli*. Hp; true woodland; common; Apr–Jul.

## Polygonaceae

*Polygonum punctatum* Ell. Hf; stream bottoms, valleys, stream currents; common; Apr–Oct.

*Eriogonum inflatum* Torr. & Frém. var. *deflatum* I. M. Johnston. Hp; valleys, open areas; rare; Feb–Apr; no voucher.

## Polygalaceae

*Polygala apopetala* Brandegee. Ab; true woodland; occasional populations; Aug–Oct.

## Primulaceae

*Samolus vagans* E. Greene. An; stream bottoms; occasional in muddy habitats; Apr–Jul.

## Podostemonaceae

*Podostemon ceratophyllum* Michx. Hf; valleys, vernal pools; locally abundant; Mar–Jun; no voucher.

## Ranunculaceae

\**Ranunculus harveyi* (A. Gray) Britton var. *australis* (Brandegee) L. Benson. Hp; stream bottoms, moist habitats; occasional; Jun–Oct.

*Ranunculus hydrocharoides* A. Gray. Hp; valleys, true woodland, moist habitats; Aug–Sep.

\**Thalictrum peninsulare* Rose. Hp; true woodland, stream bottoms; occasional; Aug–Oct.

## Rosaceae

*Alchemilla aphanoides* Mutis var. *subalpestris* Perry. Hp; valleys, true woodland; occasional in meadows and disturbed soils; Jun–Sep.

*Fragaria mexicana* Schldl. Hf; stream bottoms; locally abundant; Apr–May; “fresa”.

*Heteromeles arbutifolia* (Aiton) M. Roem. Ab; stream bottoms; occasional; Apr–Jun; “toyon”.

*Prunus serotina* Ehrh. subsp. *virens* (Wooton & Standley) McVaugh. Ar; true woodland, stream bottoms; occasional; Mar–Apr; “cerezo”.

*Rubus scolocaulon* Brandegee. Ab; stream bottoms; occasional; Apr–Jun; “zarzamora”.

## Rubiaceae

*Galium microphyllum* A. Gray. Hp; stream bottoms, true woodland; locally abundant; almost any month; (*Relbunium microphyllum* (A. Gray) Hemsl.).



*Galium uncinulatum* DC. Hp; stream bottoms, true woodland; occasional in shaded places; flowering almost all year.

*Houstonia arenaria* Rose. An; open areas, valleys, oak woodland; locally abundant in sunny and sandy areas; Aug–Nov.

*Houstonia australis* I. M. Johnston. Hp; stream bottoms, oak woodland; locally abundant in shaded places; Sep–Nov.

*Mitracarpus hirtus* (L.) DC. An; open areas, oak woodland; occasional; Aug–Nov.

*Mitracarpus linearis* Benth. An; open areas, oak woodland; less common than the preceding species; Oct–Jan?

*Mitracarpus schizangius* DC. Hp; true woodland, open areas, oak woodland; occasional in disturbed sites; Feb–Jun.

*Randia megacarpa* Brandegee. Ar; open areas, oak woodland; occasional in several conditions; Jul–Sep; “papache”.

#### Salicaceae

\**Populus brandegeei* var. *glabra* Wiggins. Ar; stream bottoms, oak woodland; locally abundant along arroyos; Feb–Mar.

*Salix lasiolepis* Benth. Ar; stream bottoms, oak woodland; less common than the preceding species; Mar–Apr; “sauce”.

#### Sapindaceae

*Dodonaea viscosa* Jacq. Ab; open areas, oak woodland; locally abundant; Apr–Aug; “guayavillo”.

#### Scrophulariaceae

*Bacopa monnieri* (L.) F. Wettst. Hf; valleys, stream bottoms; occasional in muddy habitats; any month.

*Castilleja bryantii* Brandegee. An; true woodland, stream bottoms, valleys, open areas; abundant; Nov–Feb.

*Linaria texana* Scheele. An; stream bottoms, valleys; uncommon in stream banks; Feb–May.

*Mimulus guttatus* Fisch. ex DC. Hf; valleys, stream bottoms; locally abundant along water courses; any month.

*Russelia retrorsa* E. Greene. Hp; open areas, oak woodland; uncommon in rocky habitats; Nov–Mar.

#### Solanaceae

*Solanum nodiflorum* Jacq. Ab; true woodland, stream bottoms, oak woodland; scattered populations; any month.

#### Styracaceae

*Styrax argenteus* Presl. Ar; stream bottoms; only one population found; Sep–Oct; “aguacatillo”.

#### Thymelaeaceae

*Daphnopsis* sp. (undescribed). Ab, open areas, a few populations known; Aug; “mangle de la sierra”.

#### Umbelliferae (Apiaceae)

*Arracacia brandegeei* J. Coulter & Rose. Hp; widespread beneath shade; Aug–Oct; “chuchupate”; medicinal.

*Hydrocotyle umbellata* L. Hf; valleys, along streams; abundant; May–Jul.



## Valerianaceae

*Valeriana sorbifolia* Kunth. An; stream bottoms, true woodland; locally abundant in shaded places; Oct–Dec.

## Verbenaceae

*Verbena carolina* L. Hp; true woodland, open areas, oak woodland; occasional in disturbed soils; Aug–Oct.

## Vitaceae

*Vitis peninsularis* M. E. Jones. Tl; stream bottoms, oak woodland; occasional, creeping in shaded places; May–Jun; “uva cimarrona”.

## Monocotyledones

## Agavaceae

\**Agave promontorii* Trel. Sm; open areas, oak woodland, among rocks; occasional; Dec–Mar; “mezcal”.

*Agave aurea* Brandegee. Sm; open areas, oak woodland, among rocks; less common than the preceding species; Dec–Mar; “mezcal”; no voucher.

\**Nolina beldingii* Brandegee. Ab; widespread in all oak-pine woodland communities, but not in the valleys; May; “sotol”.

## Amaryllidaceae

*Behria tenuiflora* E. Greene. Hp; widespread, dense populations are scattered; Sep–Nov.

## Bromeliaceae

*Hechtia montana* Brandegee. Hp; open areas; locally abundant; Oct–Dec; “maguey-cillo”.

## Commelinaceae

*Commelina coelestis* Willd. Hp; true woodland, stream bottoms; scattered locations; Sep–Nov.

*Commelina dianthifolia* Delile. Hp; valleys, true woodland; common; Aug–Nov.

*Gibasis heterophylla* (Brandegee) Reveal & Hess. Hp; true woodland; common; Aug–Sep.

\**Tinantia modesta* Brandegee. An; valleys, stream currents; uncommon; Sep–Oct.

\**Tradescantia peninsularis* Brandegee. Hp; oak woodland; occasional in shaded habitats; Sep.

## Cyperaceae

\**Carex lagunensis* M. E. Jones. Hf; valleys; uncommon along streams and meadows; Sep–Oct.

*Carex spissa* L. Bailey. Hf; valleys, oak woodland; along streams, occasional; Aug–Sep.

*Cyperus aristatus* Rottb. An; valleys, oak woodland; common, sandy stream banks and meadows; Aug–Oct (*C. squarrosus* L.).

*Cyperus arsenei* O'Neill & Benedict. Hf; valleys, stream bottoms, oak woodland; occasional in muddy habitats; Aug–Oct.

*Cyperus dipsaceus* Liebm. Hf; valleys, stream bottoms; occasional along streams; Aug–Oct.

*Cyperus mutisii* (Kunth) Griseb. Hf; valleys, stream bottoms; occasional along streams; Sep–Oct.



*Cyperus odoratus* L. An; valleys, other open areas, oak woodland; locally abundant; Aug–Oct (*C. ferax* L. C. Rich.).

*Cyperus pallidicolor* (Kukenth.) Tucker. Hp; valleys, true woodland, stream bottoms; occasional along streams and wet sandy areas; Sep–Oct.

*Cyperus perennis* (M. E. Jones) O'Neill. Hp; valleys, on meadows; rare; Sep.

#### Gramineae (Poaceae)

*Aegopogon cenchroides* Humb. & Bonpl. var. *breviglumis* (Scribner) Beetle. Hp; valleys, true woodland, loamy soils and shaded places; uncommon; Sep–Oct.

*Aegopogon tenellus* (DC.) Trin. An; valleys, stream bottoms, open areas, sandy soils and crevices; locally abundant; any month.

*Agrostis semiverticillata* (Forsskal) C. Chr. Hp; open areas, disturbed areas; uncommon; Sep–Oct (*Polypogon semiverticillata* (Forsskal) Hylander).

*Agrostis exarata* Trin. Hp; valleys, open areas, oak woodland; early regenerative stages; uncommon; Sep–Oct.

*Aristida schiediana* Trin. & Rupr. Hp; valleys, open areas, sunny places; occasional; Sep–Oct.

*Bouteloua hirsuta* Lagasca var. *hirsuta*. Hp; valleys, meadows; occasional; Aug–Oct.

*Bouteloua hirsuta* Lagasca var. *glandulosa* (Cerv.) Gould. Hp; valleys, meadows; abundant; Aug–Oct.

*Brachipodium mexicana* (Roemer & Schultes) Link. An; stream bottoms, shaded and wet habitats; uncommon; Aug–Dec.

*Bromus anomalus* Rupr. ex Fourn. An; stream bottoms, shaded habitats; uncommon; Aug–Dec.

*Cynodon dactylon* (L.) Pers. Hp; valleys, stream banks; locally abundant; Jul–Mar.

*Digitaria sanguinalis* (L.) Scop. Hp; valleys, stream banks; locally abundant; Aug–Dec.

*Eragrostis intermedia* A. Hitchc. var. *intermedia*. Hp; open areas, oak woodland; occasional; Aug–Nov.

*Muhlenbergia wolfii* (Vasey) Rydb. An; from collection by Brandegee in 1899; no voucher.

*Panicum bulbosum* Kunth. Hp; stream bottoms, shaded places and crevices; occasional; Jul–Oct.

*Pereilema crinitum* Presl. An; valleys, true woodland; locally abundant; Sep–Oct.

*Paspalum vaginatum* Sw. Hp; valleys, along stream banks; locally abundant; any month.

*Piptochaetium fimbriatum* (Kunth) A. Hitchc. Hp; margin of valleys, true woodland, stream bottoms; occasional beneath pines; Aug–Oct.

*Rynchelytrum repens* (Willd.) C. E. Hubb. An; open areas, oak woodland; locally abundant; Aug–Oct.

*Schizachyrium sanguineum* (Retz.) Alston var. *brevipedicellatum* (Beal) Hatch. Hp; open areas; occasional; Sep–Dec.

*Tripsacum lanceolatum* Rupr. ex Fourn. Hp; stream bottoms; locally abundant; Sep–Oct.

*Vulpia octoflora* (Walter) Rydb. var. *octoflora*. An; valleys, meadows; locally abundant; Sep–Nov (*Festuca octoflora* Walter).

#### Iridaceae

*Sisyrinchium demirsum* E. Greene. Hp; valleys, stream bottoms, along current streams; occasional; flowering any month.

#### Juncaceae

*Juncus balticus* Willd. Hf; valleys, stream bottoms, along current streams; uncommon; Sep–Jan.



- Eragrostis intermedia* A. Hitchc. var. *oreophila* (L. H. Harvey) Whitespoon. Hp; open areas, oak woodland; less common than the preceding variety; Aug–Nov?.
- Eragrostis orcuttiana* Vasey. An; valleys, meadows; occasional; Aug–Dec.
- Heteropogon contortus* (L.) Beauv. ex Roemer & Schultes. Hp; oak woodland; locally abundant; Sep–Oct; “zacate retorcido”.
- Lycurus phleoides* Kunth. Hp; valleys, meadows; common; Oct–Dec.
- Microchloa kunthii* Desv. An; valleys, meadows; abundant; Aug–Nov.
- Muhlenbergia ciliata* (Kunth) Kunth. An; from collections by Brandegee in 1893 at some valley; no voucher.
- Muhlenbergia emersleyi* Vasey. Hp; open areas, oak woodland; abundant; Aug–Nov.
- Muhlenbergia filiformis* (Thurber) Rydb. An; valleys, meadows; rare; Sep–Oct.
- Muhlenbergia microsperma* (DC.) Kunth. Hp; open areas, oak woodland; uncommon; Sep–Oct.
- Muhlenbergia repens* (Presl) A. Hitchc. Hp; open areas, oak woodland; occasional; Sep–Oct.
- Muhlenbergia rigida* (Kunth) Kunth. Hp; valleys, open areas, oak woodland; occasional; Aug–Sep.
- Muhlenbergia texana* Buckley. An; valleys, open areas, oak woodland; locally abundant; Aug–Oct.

#### Lemnaceae

- Lemna aequinoctialis* Wellw. Hf; valleys, little pools; common; Apr?.

#### Orchidaceae

- Arethusa rosea* Benth. Hp; stream bottoms; occasional, found in a few sites; Sep–Oct.
- \**Epipactis gigantea* Douglas ex Hook. Hf; stream bottoms, stream currents; rare; Jun–Jul.
- Habenaria enthomanta* (LaLlave & Lex.) Li. Hp; true woodland; uncommon; Nov–Dec.
- Habenaria clypeata* Lindl. Hp; true woodland, open areas; uncommon; Sep–Nov.
- Habenaria dilatata* (Pursh) Hook. Hp; true woodland; uncommon; Sep–Oct.
- Malaxis corymbosa* (S. Watson) Lindl. Hp; true woodland, stream bottoms, open areas; scattered locations; Sep–Oct.
- Malaxis soulei* L. O. Williams. Hp; true woodland, open areas; uncommon; Sep–Oct.
- Malaxis unifolia* Michx. Hp; true woodland, open areas; oak woodland; more common than the preceding species; Sep–Nov.
- Spiranthes cinnabarina* LaLlave & Lex. Hp; true woodland, stream bottoms; rare; Aug–Oct?.

#### Palmae (Arecaceae)

- Erythea brandegeei* Purpus. Ar; abundant at stream bottoms; Feb–Mar; “palmilla, palma azul”.
- Washingtonia robusta* H. A. Wendl. Ar; stream bottoms; uncommon here, but widespread at lower elevations; May–Jun; “palma real”.

#### Potamogetonaceae

- Potamogeton foliosus* Raf. Hf; valleys, vernal pools; locally abundant; Jul–Aug.
- Potamogeton illinoensis* Morong. Hf; valleys, oak woodland; locally abundant in vernal pools; May–Jul.



# ECOLOGY AND DISTRIBUTION OF *PINUS LAGUNAE*, IN THE SIERRA DE LA LAGUNA, BAJA CALIFORNIA SUR, MEXICO

MARIE-FRANÇOISE PASSINI and NICOLE PINEL  
Laboratoire de Botanique Tropicale,  
Université Pierre et Marie Curie,  
12 rue Cuvier, 75005, Paris, France

## ABSTRACT

*Pinus lagunae* extends from 1200 to 2000 m only on the Sierra de la Laguna, Baja California Sur, Mexico. This study provides descriptions of habitat, soil characteristics, composition and cover of herbaceous vegetation, and physiography. Three forest types are described: one of *Pinus lagunae* only, the others with *Pinus lagunae* and *Quercus devia*.

## RESUMEN

*Pinus lagunae* se encuentra unicamente entre los 1200 y 2000 m en la Sierra de la Laguna, Baja California Sur, México. Este estudio se propone descripciones del habitat, característicos del suelo, composición y cubierta de la vegetación herbacea, y fisiographía. Tres bosques han sido descritos: uno exclusivamente formado por *Pinus lagunae* y los otros formados con *Pinus lagunae* y *Quercus devia*.

*Pinus lagunae* (Robert-Passini) M.-F. Passini is found in a limited area in the Sierra de la Laguna at the southern end of the Baja California peninsula (Baja California Sur, Mexico). In 1981, Robert-Passini described it as a variety of *Pinus cembroides* Zucc. In 1983, D. K. Bailey gave it subspecific rank and in 1987, M.-F. Passini raised it to specific level. This article describes the ecology and floristic composition of *Pinus lagunae* communities.

## METHODS

Ecological and floristic surveys (Tables 1, 2) were made at the summit of Sierra de la Laguna (Figs. 1, 2) along three transects: north to south between La Victoria and San Francisquito (Fig. 2, transect 1-1'), northwest to southeast between Cerro el Picacho and Cañon de la Zorra, and west to east between Cañon de la Burrera and Cañon de la Zorra. Ecological variables and floristic composition were noted in samples of  $25 \times 20 \text{ m}^2$ . The ecological variables include geographic sites, altitude, topographic exposure, slope and substrate, surface percentage of hard stone, loose gravel, fine soil, and litter, and variation in vegetation: trees, shrubs and herbaceous layer density (Godron et al. 1968; Passini 1982).



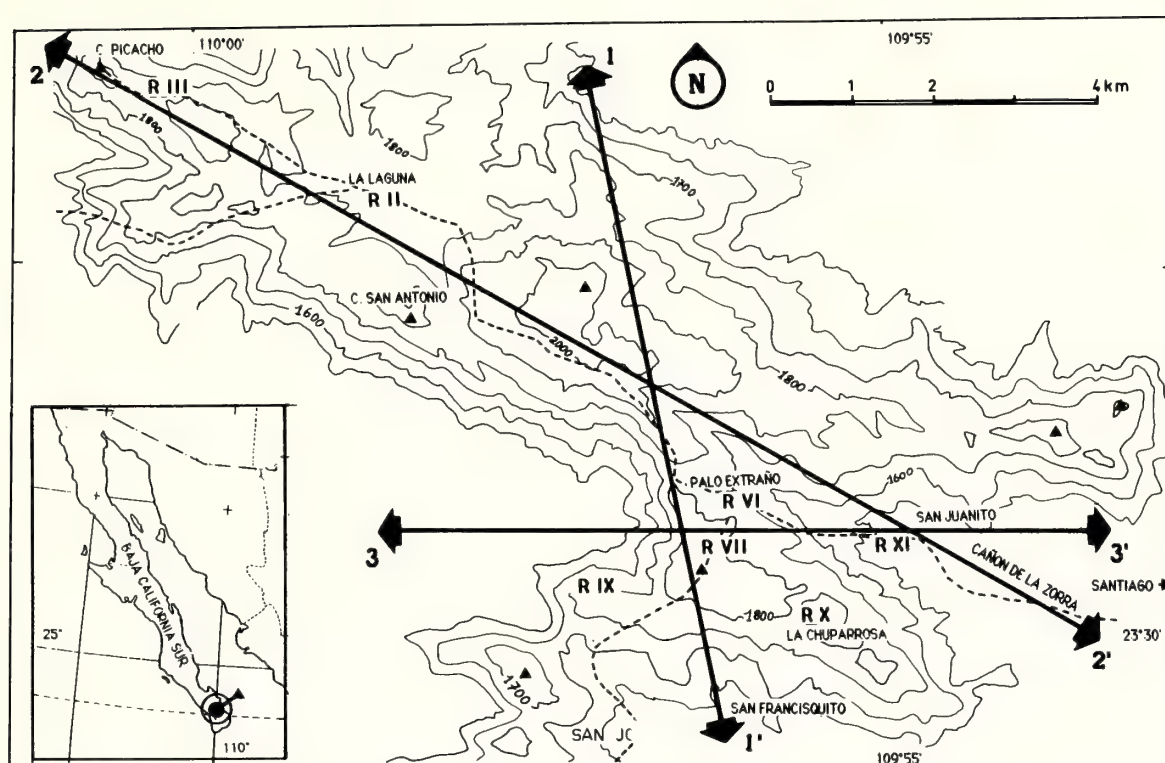


FIG. 1. The Sierra de la Laguna. Lines 1-1', 2-2', and 3-3' are transects discussed in text and illustrated in Fig. 2.

Trees were defined as plants more than 2 m high, having a definite trunk and nonramified at the base. Stand density was calculated according to Robert (1973), who considered forests to be highly dense if the distance "d" between trunks is less than 3 m, dense if d is between 3 and 8 m, and open if d is between 8 and 15 m.

Each species was given an abundance coefficient from 1 to 5. Specimens of plant collections were placed at the Herbaria at the Department of Terrestrial Biology of Centro de Investigaciones Biológicas (Comitán), La Paz, Baja California Sur, and the Laboratoire de Botanique Tropicale in Paris.

#### GEOGRAPHY AND ECOLOGICAL CONDITIONS

The Sierra de la Laguna, situated between 23°35' and 23°25'N, 105°50' and 110°W, is a deeply dissected range with coarse granitic soil derived from batholithic bedrock dating to the Cretaceous period (Durham and Allison 1969). These mountains appeared in the Tertiary period when the peninsula separated from the American continent. Faulting brought about an eastward tilt to the mountain block with a steep escarpment on the west flank and gentler slopes toward the Gulf of California. The soils, derived from granite parent rock, are slightly acid (pH varying from 5 to 7) and have an alluvial-sandy texture throughout the Sierra.

Annual rainfall varies from 200 mm to 800 mm, mostly between July and October with a mean of 580 mm (Reygadas and Velazquez



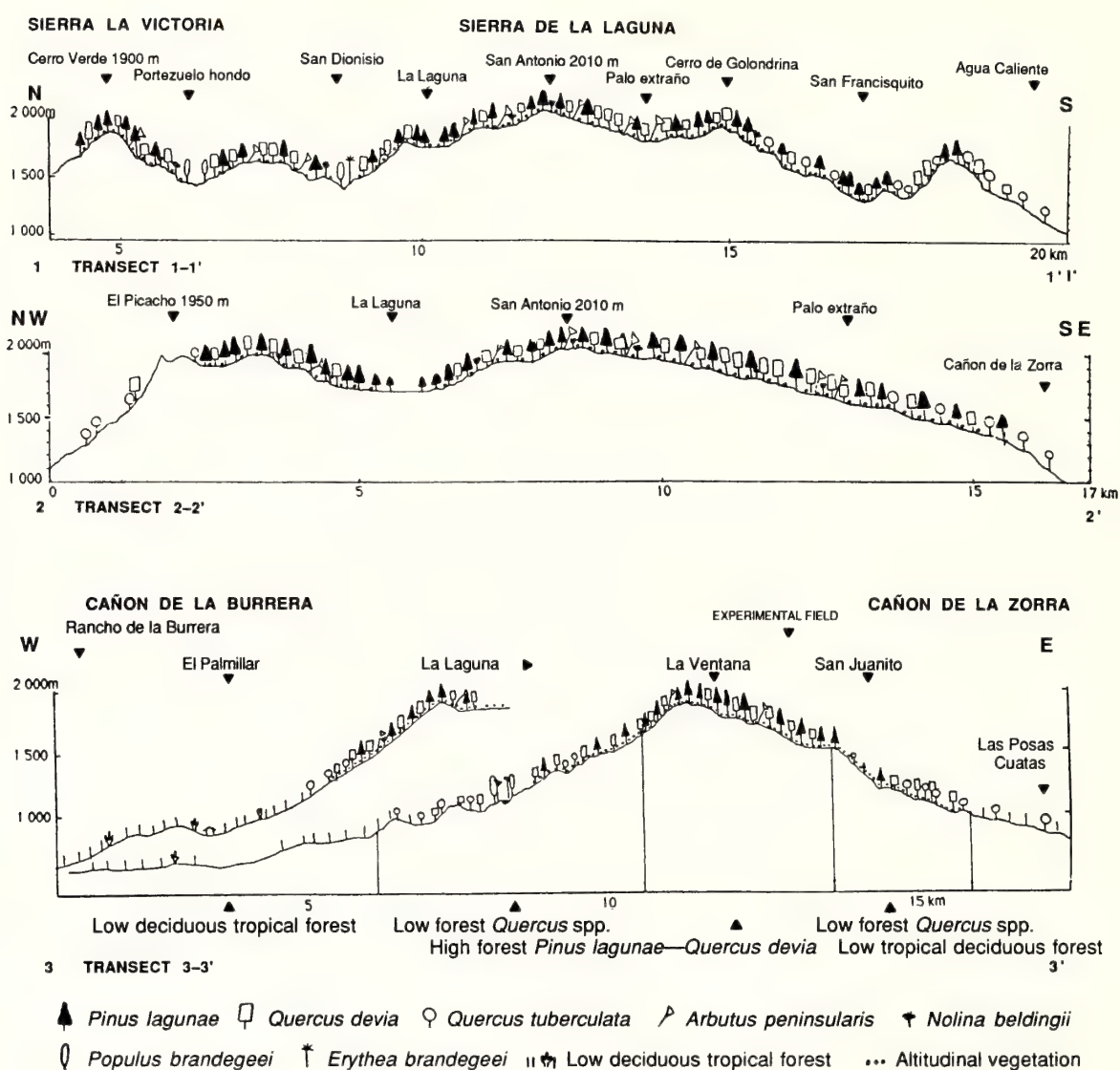


FIG. 2. Altitudinal distribution of *Pinus lagunae* and *Quercus devia* along three transects (see Fig. 1).

1981). Annual amounts are much greater when there are hurricanes. Extremely violent rainfalls during such storms (70 mm per hour in 1979) wash away earth, rocks, sand, and vegetation, leaving little water for vegetation. Slight rainfall during January and February accounts for 5% of the annual rainfall. Winter fog is frequent on the Sierra summit.

The average annual temperature is 18.9°C (Reygadas and Velazquez 1981) ranging from 25°C in July to 11.9°C in January. Temperatures occasionally drop below 0°C in December, January, and February. The daily average temperature is 29°C in January, and 14°C in September and October.

#### ALTITUDINAL DISTRIBUTION OF *PINUS LAGUNAE*

On the western slope of Sierra de la Laguna (Fig. 2, transect 3-3'), isolated pines occur at 1300 m, in the Cañon de la Burrera,



TABLE 1. CHARACTERISTICS OF SEVEN SAMPLE SITES IN THE SIERRA DE LA LAGUNA, BAJA CALIFORNIA SUR. <sup>1</sup> Soil pH was measured at a depth of 0–10 cm with a Hellige pH meter.

| Site number                       |                      |                          |                             |                      |                            |                      |                            |  |  |  |
|-----------------------------------|----------------------|--------------------------|-----------------------------|----------------------|----------------------------|----------------------|----------------------------|--|--|--|
|                                   | II                   | III                      | VI                          | VII                  | IX                         | X                    | XI                         |  |  |  |
| Date                              | 12 Oct 1984          | 2 May 1985               | 14 Oct 1984                 | 8 Nov 1985           | 29 Mar 1985                | 10 May 1985          | 7 May 1985                 |  |  |  |
| Location                          | La Laguna            | El Picacho               | Palo-Extraño                | Experimental         | San Franciscoquito         | La Chuparroza        | San Juanito                |  |  |  |
| Elevation (m)                     | 1700                 | 1950                     | 1650                        | 1750                 | 1700                       | 1725                 | 1400                       |  |  |  |
| Topography                        | open bowl            | main ridge               | moderate slope              | high ridge           | slope                      |                      | slope                      |  |  |  |
| Exposure                          | all                  | SE                       | E                           | NW                   | S                          | all                  | SE                         |  |  |  |
| Slope                             | 0%                   | 10%                      | 10%                         | 10%                  | 30%                        | 0%                   | 30%                        |  |  |  |
| inclination                       |                      |                          |                             |                      |                            |                      |                            |  |  |  |
| pH <sup>1</sup>                   | 5                    | 6                        | 5                           | 5                    | 7                          | 4.5                  | 5                          |  |  |  |
| Dominance 1                       | <i>Pinus lagunae</i> | <i>Quercus devia</i>     | <i>Quercus devia</i>        | <i>Quercus devia</i> | <i>Quercus devia</i>       | <i>Pinus lagunae</i> | <i>Quercus tuberculata</i> |  |  |  |
| Dominance 2                       | <i>Quercus devia</i> | <i>Rumfordia connata</i> | <i>Arbutus peninsularis</i> | <i>Pinus lagunae</i> | <i>Quercus tuberculata</i> | <i>Quercus devia</i> | <i>Pinus lagunae</i>       |  |  |  |
| Percent cover by vegetation types |                      |                          |                             |                      |                            |                      |                            |  |  |  |
| Trees                             | 25                   | 0                        | 60                          | 60                   | 80                         | 30                   | 50                         |  |  |  |
| Shrubs                            | 60                   | 80                       | 80                          | 30                   | 20                         | 20                   | 10                         |  |  |  |
| Grasses                           | 80                   | 30                       | 60                          | 20                   | 60                         | 80                   | 90                         |  |  |  |



TABLE 2. PLANTS ENCOUNTERED IN THE TWO PRINCIPAL FOREST TYPES OF THE SIERRA DE LA LAGUNA, BAJA CALIFORNIA SUR. Abundance was estimated on a scale of 1 to 5 with 5 the most abundant.

| Height class | Tall open forest of <i>Pinus lagunae</i>               | Abundance | Tall dense forest of <i>P. lagunae</i> and <i>Quercus devia</i> | Abundance |
|--------------|--|-----------|---|-----------|
| >12 m        | <i>Pinus lagunae</i> (Robert-Passini) M.-F. Passini    | 2         | <i>Pinus lagunae</i>  | 1         |
| 8-12 m       | —  | —         | <i>Quercus devia</i> Goldman                                    | 2         |
| 4-8 m        | <i>Arbutus peninsularis</i> Rose & Goldman             | 1         | <i>Pinus lagunae</i>  | 3         |
| 2-4 m        | —  | —         | —   | —         |
| 1-2 m        | —  | —         | <i>Garrya salicifolia</i> Eastw.                                | 1         |
|              |  |           | <i>Nolina beltingii</i> Brandegee                               | 1         |
|              |  |           | <i>Lepechinia hastata</i> (A. Gray) Epling                      | 4         |
|              |  |           | <i>Rumfordia connata</i> Brandegee                              | 3         |
|              |  |           | <i>Tagetes lacera</i> Brandegee                                 | 3         |
| 0.5-1 m      | <i>Lepechinia hastata</i>                              | 3         | <i>Muhlenbergia microserma</i> (DC.) Kunth                      | 3         |
|              | <i>Arracacia brandegeei</i> J. Coulter & Rose          | 1         | <i>Stachys coccinea</i> Jacq.                                   | 2         |
|              | <i>Calliandra brandegeei</i> (Britton & Rose) Gentry   | 1         | <i>Bromus anomalus</i> Rupr. ex Fourn.                          | 2         |
|              | <i>Erythea brandegeei</i> Purpus                       | 1         | <i>Acalypha comoudana</i> Millsp.                               | 1         |
|              | <i>Muhlenbergia rigida</i> (Kunth) Kunth               | 1         | —   | —         |
|              | <i>Opuntia lagunae</i> K. Brandegee                    | 1         |   |           |
|              | <i>Rhus integrifolia</i> (Nutt.) Benth. & Hook.        | 1         |   |           |
|              | <i>Tagetes lacera</i>                                  | 1         |   |           |
| 25-50 cm     | <i>Bidens nudata</i> Brandegee                         | 4         | <i>Calliandra brandegeei</i>                                    | 2         |
|              | <i>Tagetes lacera</i>                                  | 3         | —   | —         |
|              | <i>Piptochaetium fimbriatum</i> (Kunth.) Hitchc.       | 2         |   |           |
|              | <i>Brachypodium mexicanum</i> (Roemer & Schultes) Link | 1         |   |           |



TABLE 2. CONTINUED.

| Height class | Tall open forest of <i>Pinus lagunae</i>      | Abundance | Tall dense forest of <i>P. lagunae</i> and <i>Quercus devia</i> | Abundance |
|--------------|---|-----------|---|-----------|
| 2-25 cm      | <i>Agrostis</i> sp.                           | 4         | <i>Arracacia brandegeei</i>                                     | 3         |
|              | <i>Aristida schiediana</i> Trin. & Rupr.      | 4         | <i>Lupinus</i> sp.  | 2         |
|              | <i>Bidens nudata</i>                          | 3         | <i>Asplenium blepharodes</i> D. Eaton                           | 1         |
|              | <i>Heterosperma xantii</i> A. Gray            | 3         | <i>Phaseolus</i> sp.  | 1         |
|              | <i>Lycurus phleoides</i> Kunth                | 3         | —   | —         |
|              | <i>Aegopogon tenellus</i> (DC.) Trin.         | 2         |   |           |
|              | <i>Bidens lemmonii</i> A. Gray                | 2         |   |           |
|              | <i>Desmodium neomexicanum</i> A. Gray         | 2         |   |           |
|              | <i>Gnaphalium</i> sp.                         | 2         |   |           |
|              | <i>Helianthemum glomeratum</i> Lagasca ex DC. | 2         |   |           |
|              | <i>Hypericum peninsulare</i> Eastw.           | 2         |   |           |
|              | <i>Muhlenbergia microsperma</i>               | 2         |   |           |
|              | <i>Arracacia brandegeei</i>                   | 1         |   |           |
|              | <i>Opuntia lagunae</i>                        | 1         |   |           |
|              | <i>Quercus devia</i>                          | 1         |   |           |
| 0-5 cm       | <i>Piptochaetium fimbriatum</i>               | 2         | <i>Arracacia brandegeei</i>                                     | 1         |
|              | <i>Cyclanthera tamnoides</i> Cogn.            | 1         |   |           |
|              | <i>Oenothera</i> sp.                          | 1         |   |           |
|              | <i>Pinus lagunae</i>                          | 1         |   |           |
|              | <i>Prunus</i> sp.                             | 1         |   |           |





FIG. 3. Tall dense forest of *Pinus lagunae* and *Quercus devia*. 1, *Pinus lagunae*; 2, *Quercus devia*; 3, *Arbutus peninsularis*; 4, *Nolina beldingii*; 5, *Lepechinia hastata*; 6, *Rumfordia connata*; 7, *Acacia peninsularis*; 8, *Muhlenbergia* sp.

growing with *Erythea brandegeei*, *Populus brandegeei*, and *Salix* sp., in an association similar to the "bosque en galería" described by Rzedowski (1978). Two-hundred-year-old pines are found at 1500 m with low, open stands of *Quercus tuberculata* and *Dodonaea viscosa*. On the east slope, small *Pinus lagunae* (<5 m) grow in isolated groves between 1200 and 1500 m. Extensive forests grow with *Quercus devia* above 1600 m.

The southern limit of pine is near Cañon San Jorge at 1700 m. *Pinus lagunae* is absent from *Quercus devia* stands, on open, sunny southern exposures from Cañon de Agua Caliente (Fig. 2, transect 1-1'). It is also absent from southern exposures in the Sierra San Lazaro and San Lorenzo at 1700 m. *Quercus devia* may withstand more xeric conditions than *Pinus lagunae*.

#### PINUS LAGUNAE FOREST TYPES

Ecologic (Table 1) and floristic surveys (Table 2) show *Pinus lagunae* vegetation to consist of 1) tall, open *Pinus lagunae* forests; 2) tall, dense *Pinus lagunae* forests with *Quercus devia*; and 3) low,



open *Pinus lagunae* forests with understory of *Quercus devia* and *Quercus tuberculata*.

1. The tall, open *Pinus lagunae* forests can be seen above 1700 m, on level, sandy basins (Fig. 2, sec. 2) or on the rounded summits of Sierra de la Laguna. Trunks average 8 m apart. *Pinus lagunae* has a pyramid shaped crown, 12 to 18 m high; first branches are about 2 m above ground. There is little shrub growth but the herbaceous layer (0–1 m high) is diverse especially after the rainy season. Dominant species, including *Bidens* sp., *Castilleja bryantii*, *Dalea* sp., *Desmodium neomexicanum*, *Helianthemum glomeratum*, *Hypericum peninsulare*, *Linanthus nuttallii*, and *Stachys coccinea*, disappear between December and July. They are replaced by a “pastizal” of Gramineae, including *Agrostis exarata*, *Agrostis semiverticillata*, *Aegopogon tenellus*, *Aristida schiediana*, *Bouteloua hirsuta*, *Lycurus phleoides*, *Muhlenbergia microsperma*, *Muhlenbergia rigida*, and *Piptochaetium fimbriatum*.

2. The tall, dense *Pinus lagunae* and *Quercus devia* dominant formations prevail on steeper upper flanks of the Sierra de la Laguna (Fig. 3). Trunks average 5 m apart. Individual trees of *Pinus lagunae* have longer boles than in open forest areas on the summit. The first branches are at 3 to 7 m above ground. Pine diameters vary from 32 to 58 cm ( $n = 50$ ; mean = 45 cm). Annual rings from wood samples taken by a Pressler auger show that 34-cm-diameter pines average 60 years of age. Numerous young 0.5–2-m trees can be seen in open spaces, 50–200 per hectare. *Quercus devia* has an average height of 10 m and an average diameter of 40 cm. Three hundred specimens form 35% coverage on the experimental site. Contiguous cover of this species protects shrub layer growth during the dry season. It sheds its leaves in late February, flowers in March, and is in full growth by the end of March. Acorns ripen in September. Other trees in this type include *Arbutus peninsularis* (madroño, 5 m) and *Nolina beltingii* (2 to 4 m). A dense shrub layer is dominated by *Lepechinia hastata*, *Rumfordia connata*, *Tagetes lacera*, *Calliandra brandegeei*, and *Acacia peninsularis*.

The herbaceous layer, though less dense and less rich than in the previous type, includes a number of Gramineae: *Agrostis* sp., *Aristida schiediana*, *Piptochaetium fimbriatum*, *Muhlenbergia emersleyi*, *Perilema crinitum*, *Schizachyrium* sp., and *Stipa* sp. Species other than the Gramineae are the same as those encountered in tall *Pinus lagunae* dominant forests.

3. Low open forests of *Pinus lagunae*, *Quercus devia*, and *Quercus tuberculata* are found on the lower edge of the previous type. It represents the ecotone between *Pinus lagunae* and *Quercus devia* forests. Pines have a more stunted habit, growing no higher than 12 m. The shrub layer includes *Croton* sp., *Dodonaea viscosa*, and *Rhus integrifolia*. The herbaceous layer is mainly made up of Gramineae.



## SUMMARY

*Pinus lagunae* appears above 1200 m in Sierra de la Laguna which represents one of the lowest altitudinal limits observed among pines in the "cembroides group". *Pinus lagunae* stands fall into three types: a low thin forest of *Pinus lagunae* and *Quercus tuberculata* below 1500 m, a tall dense stand of *Pinus lagunae* and *Quercus devia*, found throughout the Sierra above 1500 m on the summit, and a tall open *Pinus lagunae* forest. *Pinus lagunae* display maximum growth rate and seed production in the latter type.

## ACKNOWLEDGMENTS

This study was part of the research program on xeric pine formations led by Passini. Field studies were conducted by Nicole Pinel, from October 1984 until July 1985, in collaboration with the "Centro de Investigaciones Biologicas" de La Paz (C.I.B.) and the "Instituto Nacional de Investigaciones Forestales" (I.N.I.F.), Todos Santos (Baja California Sur). The authors are grateful to Annetta Carter, Richard A. Minnich, and David J. Keil, for their numerous helpful comments.

## LITERATURE CITED

- BAGNOULS, F. and H. GAUSSEN. 1953. Saison sèche et indice xérothermique. Bull. Soc. Hist. Toulouse 88:193-239.
- BAILEY, D. K. 1983. A new allopatric segregate from and a new combination in *Pinus cembroides* Zucc. at its southern limits. Phytologia 54:89-99.
- DURHAM, J. W. and E. ALLISON. 1960. The geologic history of Baja California and its marine faunas. In Symposium: The biogeography of Baja California adjacent seas, Syst. Zool. 9:47-91.
- GODRON, M., et al. 1968. Relevé méthodique de la végétation et du milieu. C.N.R.S., Paris, 292 pp.
- PASSINI, M.-F. 1982. Les forêts de *Pinus cembroides* au Mexique, étude phytogéographique et écologique. Ed. Recherches sur les Civilisations, Paris. 374 pp.
- . 1987. The endemic pinyon of Lower California: *Pinus lagunae* M.-F. Passini. Phytologia 63:337-338.
- PINEL, N. 1985. La formation à *Pinus cembroides* var. *lagunae* dans la Sierra de la Laguna, Basse Californie, Mexique. Rapport stage de Diplôme d'Etudes Approfondies, Toulouse.
- REYGADAS and VELAZQUEZ. 1981. Aporte energético y climatológico en la Sierra de la Laguna, Baja California Sur. Informe general del Centro de Investigaciones Biologicas, La Paz, pp. 235-243.
- ROBERT, M.-F. 1973. Contribution à l'étude des forêts de *Pinus cembroides* dans l'est du Mexique. Thèse de 3ème cycle, Montpellier. 131 pp.
- ROBERT-PASSINI, M.-F. 1981. Deux nouveaux pins pignons du Mexique. Bull. Mus. Hist. Natn., Paris, 4, 3, sect. B, Adansonia 1:61-73.
- RZEDOWSKI, J. 1978. Vegetación de México, Ed. Limusa, México. 432 pp.
- SHREVE, F. and I. L. WIGGINS. 1964. Vegetation and flora of the Sonoran desert, Vol. I. Stanford University Press. 839 pp.

(Received 4 Jan 1988; revision accepted 28 Oct 1988.)



# POSTFIRE VEGETATION DEVELOPMENT IN THE COSTA RICAN PARAMOS

SALLY P. HORN

Department of Geography and Graduate Program in Ecology,  
The University of Tennessee,  
Knoxville, TN 37996-1420

## ABSTRACT

Postfire vegetation development was studied at four recent burn sites within the grass- and shrub-dominated páramos of the Cordillera de Talamanca, Costa Rica. The bamboo *Swallenochloa subtessellata* and the ericaceous shrubs *Vaccinium consanguineum* and *Pernetia coriacea* resprout vigorously after fire, but the shrub *Hypericum irazuense* suffers high mortality and reestablishes by seed. Herbs and shrubs are slow to colonize openings created by fire, and bare patches of ground persist for a decade or more following burning. Regenerating bamboo clumps regain prefire heights of 1–2 m within ten years, but associated shrubs require more than a decade to regain comparable preburn statures.

## RESUMEN

Se estudió el desarrollo de vegetación en cuatro sitios quemados después de unos incendios en los páramos dominados por gramíneas y arbustos de la Cordillera de Talamanca, Costa Rica. El bambú *Swallenochloa subtessellata* y las ericáceas *Vaccinium consanguineum* y *Pernetia coriacea* se retoñan vigorosamente después de quemarse, pero el arbusto *Hypericum irazuense* sufre alta mortalidad, y se reestablece por semillas. Colonización por hierbas y arbustos avanza lentamente, y sitios de tierra sin cubierta vegetal persisten por una década o más. Los bambús quemados reponen su altura original de 1–2 m dentro de diez años, pero los arbustos necesitan más de una década para recuperar estaturas comparables.

The grass- and shrub-dominated vegetation found above timberline in the Cordillera de Talamanca, Costa Rica, shows close botanical affinity with the Andean páramos, and is generally regarded as representing the northernmost extent of páramo vegetation in the neotropics (Weber 1959; Cuatrecasas 1979; Lauer 1981). Like their South American counterparts, the Costa Rican páramos have been subjected to considerable human disturbance, including repeated burning. Carelessly tossed matches and cigarettes, arson, and helicopter and airplane crashes are among the sources of recent páramo fires. The high incidence of thunderstorm activity in Costa Rica (World Meteorological Organization 1953, 1956) suggests that lightning may also serve as an ignition source; however, there are as yet no documented cases of lightning-set fires.



The impact of burning on neotropical páramo vegetation has received little attention. Grubb (1970) discussed changes in herbaceous cover following human-set fires in the páramo of Cerro Antisana, Ecuador, and Smith (1981) described damage to rosettes of *Espletia shultzii* Wedd. caused by burning in a Venezuelan páramo. In Costa Rica, Janzen (1973a) studied vegetation recovery following a 1969 fire on Cerro Asunción. He provided data on regeneration rates for the dominant woody dicots, but did not examine differences in survivorship. More recently, Williamson et al. (1986) monitored patterns of postfire vegetation recovery on nearby Cerro Zacatales. Their study revealed evidence of differential shrub mortality, which they related to fire history. Chaverri and associates (1976) established quadrats within the páramo of Chirripó National Park, Costa Rica following a major wildfire in March of 1976, but the results of their long-term study have not yet been published.

### STUDY AREAS

Studies of postfire regeneration were carried out in the highlands surrounding Cerro Chirripó (3819 m), the highest point in Costa Rica, and near Cerro Buenavista (3491 m) along the Inter-American highway crossing in the northwestern end of the Cordillera de Talamanca (Fig. 1). The granitic rocks that form the backbone of the cordillera are exposed near Cerro Chirripó but mantled by basalts and pyroclastic deposits in the Buenavista massif (Weyl 1957). Soils in both areas are generally well-drained, rich in organic matter, and acidic, with pH values as low as 4.0 (Otárola 1976). Soil depths range from a few centimeters on the summits of the peaks to over 50 cm near the upper forest limit. Glaciers occupied the upper portions of valleys in the Chirripó highlands during the Pleistocene (Hastenrath 1973), leaving behind a scenic ice-carved landscape that was part of the impetus to declare the area a national park. The slightly lower Buenavista massif was apparently not glaciated (Hastenrath 1963).

Meteorological data from the Buenavista highlands (Table 1) show a mean annual temperature of 7.6°C and an annual rainfall total of about 2500 mm. Nearly 90% of the total precipitation falls during the May to November wet season. Afternoon clouds characteristically enshroud the Talamancan highlands, and high atmospheric humidity moderates the dry season. But for weeks or months during the dry season the condensation belt lies below timberline, and the páramos experience clear, dry weather. Grasses, sedges, and some herbaceous dicots die back at this time, and ground litter dries out, providing the fuel for fires.

The vegetation of the Chirripó and Buenavista páramos has been described by Weber (1959). Grasses, perennial herbs, and evergreen



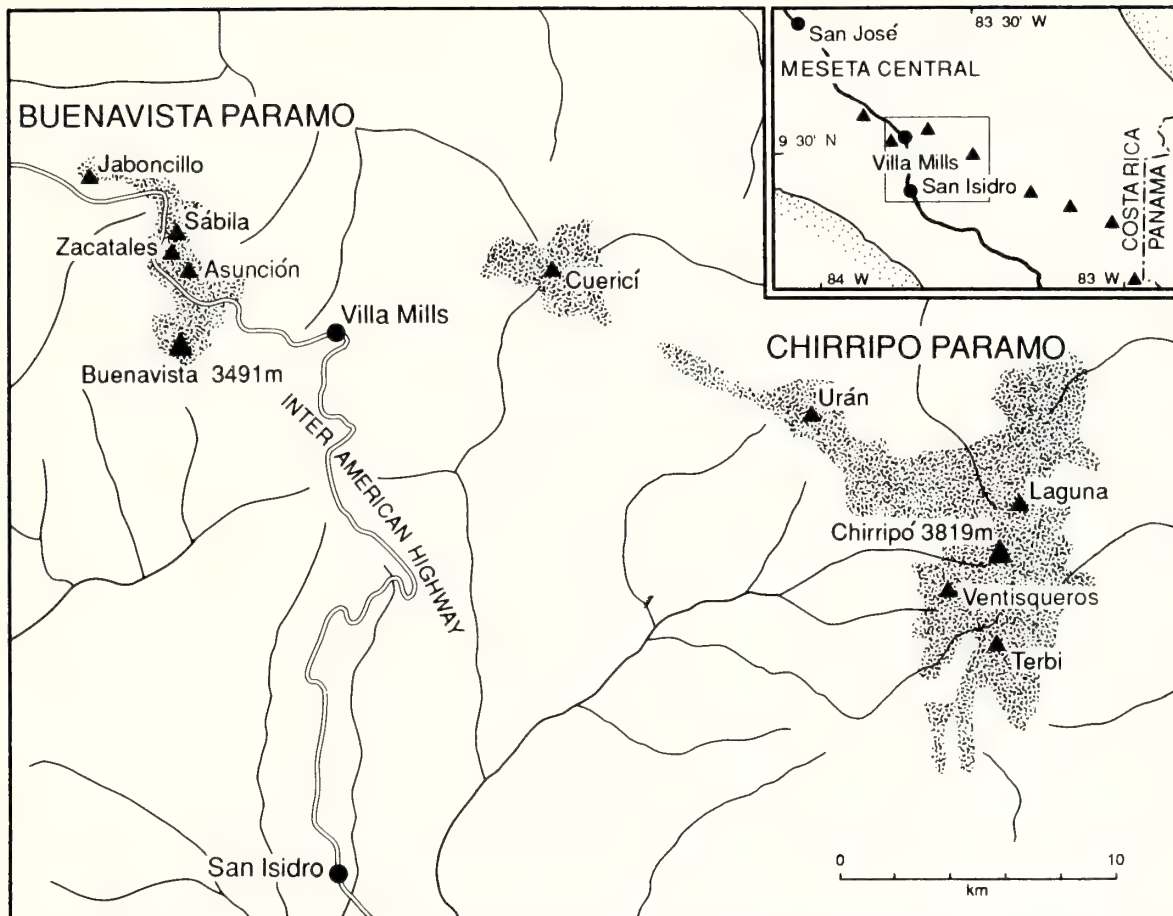


FIG. 1. Map showing the location of study areas in the Cordillera de Talamanca, Costa Rica. Shading indicates the approximate present distribution of páramo vegetation. Triangles in inset map are major peaks along the crest of the range. Based on field observations and the 1:50,000 topographic maps published by the Instituto Geográfico Nacional.

shrubs cover all areas above 3300 m, and extend as low as 3150 m in some areas. The montane forests that replace the páramo at its lower elevational limit are dominated by the oak *Quercus costaricensis* Liebm. The most characteristic páramo species is the bamboo *Swallenochloa subtessellata* (Janzen 1983), which often occurs in nearly monospecific stands. Intermixed with the bamboo grow several small-leaved, evergreen shrubs, with the families Hypericaceae, Compositae, and Ericaceae particularly well represented. Grasses, sedges, herbaceous dicots, and club mosses occur sparsely in the understory of the shrub layer, and in dense swards where the canopy is more open.

Vegetation patterns in both areas reflect a long history of human disturbance. The presence of large cut stumps and charred snags of *Escallonia poasana* and *Arctostaphylos arbutoides* (Lindl.) Hemsl. on Cerro Zacatales and Cerro Asunción indicates that small trees or large shrubs once grew higher on the slopes of the Buenavista massif. Clearing and burning has enlarged the Buenavista páramo and may even have initially created it (Janzen 1973a, b, 1983). During 1985 I observed only a few cattle in the Buenavista páramo, but grazing



TABLE 1. CLIMATIC DATA, CERRO PARAMO METEOROLOGICAL STATION (3475 m), BUENAVISTA HIGHLANDS, COSTA RICA. Temperature data are from the period 1971–1979; precipitation data are from the period 1971–1984. Compiled from unpublished records on file in the Departamento de Estudios Básicos, Instituto Costarricense de Electricidad, San José, Costa Rica (station 073080). The station elevation is incorrectly listed in the records as 3365 m.

|              | Temperature (in °C)   |                       |                 | Precipitation<br>(in mm) |
|--------------|-----------------------|-----------------------|-----------------|--------------------------|
|              | Mean daily<br>minimum | Mean daily<br>maximum | Monthly<br>mean | Mean monthly<br>total    |
| January      | 3.0                   | 10.5                  | 6.8             | 31.7                     |
| February     | 3.2                   | 11.3                  | 7.3             | 26.0                     |
| March        | 3.7                   | 12.2                  | 8.0             | 28.4                     |
| April        | 4.2                   | 12.2                  | 8.2             | 105.1                    |
| May          | 4.8                   | 11.6                  | 8.2             | 367.4                    |
| June         | 4.6                   | 11.0                  | 7.8             | 344.0                    |
| July         | 4.2                   | 10.3                  | 7.3             | 213.0                    |
| August       | 4.3                   | 10.6                  | 7.5             | 365.2                    |
| September    | 4.5                   | 10.6                  | 7.6             | 384.2                    |
| October      | 4.6                   | 10.7                  | 7.7             | 367.6                    |
| November     | 4.2                   | 10.3                  | 7.3             | 216.2                    |
| December     | 3.4                   | 10.3                  | 6.9             | 78.1                     |
| Annual mean  | 4.1                   | 11.0                  | 7.6             |                          |
| Annual total |                       |                       |                 | 2526.9                   |

seems to have been more significant in the past, and some of the clearing and burning may have been carried out to encourage herbaceous forage.

In the more isolated Chirripó massif the absence of trees is generally regarded as the natural condition (Hartshorn 1983). Clearing and grazing (by horses) is minor and is restricted to a few heavily used campsites, but human-set fires occur frequently throughout the páramo. The charcoal stratigraphy of a 110-cm sediment core from a glacial lake revealed that fires due to human activity or lightning have affected the highland for over 4000 years (Horn 1989a).

## METHODS

Postfire vegetation recovery was monitored at four páramo burn sites in late 1984 and early 1985 using line and belt transects. The number and arrangement of transects varied depending on the size of the burn and available field time, but these variations do not affect the analysis. The slow rate of organic matter decay in the Talamanca páramos was an asset to the study, because persistent fire-killed shrub and bamboo stems could be used to reconstruct the species composition and general stature of the preburn woody vegetation.

Shrub and herb cover were measured separately along random transects using the line intercept method (Bauer 1943). The cover



estimates for the herb layer included all herbs, ferns, club mosses, true mosses, and the low ericaceous shrub *Pernetia prostrata*, which is generally only 10–20 cm high; the cover estimates for the shrub layer included all larger shrubs and bamboo. At the Conejos, Zacatales, and Sábila burn sites I used six 100-m transects to estimate shrub cover (canopy projection) and five (Conejos) or six 20-m transects to estimate herb cover. At the smaller Tower 65 site I used twenty 20-m transects for shrub cover and six for herb cover.

At the larger burn sites, data on shrub and bamboo density, fire response, and prefire and postfire plant stature were collected in 2-m-wide belt transects centered on the lines used for the cover analysis. The total area sampled was 400 m<sup>2</sup> at the Zacatales site, 600 m<sup>2</sup> at the Sábila site, and 1200 m<sup>2</sup> at the Conejos site. Bamboos at the latter site were tallied in all transects but measured only in the first three. At the Zacatales site, resprouting plants were measured in additional belt transects covering 800 m<sup>2</sup>. The Tower 65 data were collected in five contiguous 5 × 20-m belt transects.

Following methods adapted from Williamson et al. (1986), I classified all living and dead shrubs and bamboo within the sample areas with prefire or postfire heights of at least 40 cm into one of four fire response categories: 1) “dead,” for plants that had been killed by the fire; 2) “resprouter,” for plants that had suffered crown loss but had subsequently resprouted; 3) “postfire colonist,” for plants that showed no evidence of having burned in the fire and that presumably had become established after the fire occurred; and 4) “fire survivor,” for plants that had survived the fire with minimal crown loss. Plants in the latter category showed evidence of scorching, which provided a means to separate them from postfire colonists. Dead plants could be identified to species based on stem architecture and the color and texture of their bark and wood. Dead plants killed in earlier fires were distinguished based on bark weathering and were tallied separately. Dead plants not killed by burning were seen rarely; these were also tallied separately.

For the woody dicots, each well-defined cluster of stems was regarded as a separate individual, except in cases where root connections were clearly present. For the clump-forming dwarf bamboo *Swallenochloa subtessellata*, each distinct clump was counted as one plant. Closely spaced clumps were counted as different plants if they were separated by at least 75 cm of ground that was devoid of dead or live culms. In practice, these criteria probably overestimated the number of separate plants, since underground stems and root systems can extend for several meters. However, without excavating every plant it was impossible to be certain whether such underground connections existed, so decisions as to what constituted an individual plant had to rest on the spacing of aboveground stems.

The highest leaf or stem of all plants in the “postfire colonist,”



“resprouter,” and “fire survivor” classes was measured to the nearest cm, and the prefire height of all “dead” and “resprouter” plants was estimated by measuring the highest dead stem. The heights of broken stems were recorded separately and excluded from calculations. The number of dead and/or live stems at the base of each shrub and the basal diameter of the largest of each type of stem were recorded. Where present, older dead stems were measured and tallied separately. For the bamboos, live culms were measured and classed by abundance (<50, 50–100, >100).

Published and unpublished reports (cited below) and field evidence provided dates for some of the fires; age estimates for other burns and for earlier fires at all burn sites were made by examining growth rings in stems of resprouting *Vaccinium consanguineum* shrubs. Ring counts in stems regenerating after fires of known age suggest that this plant produces annual rings under the seasonal precipitation regime that characterizes the Talamancan highlands. Because not all stems resprout in the first year after burning, the ring counts indicate minimum fire recurrence intervals. Voucher specimens were deposited at UC, WIS, CR, and IA (grasses only).

#### SITE DESCRIPTIONS

*Tower 65 site.* The Tower 65 burn site was located at an elevation of 3310 m on the crest of a ridge extending northeastward from Cerro Buenavista. About a year before sampling a small fire had burned roughly one-tenth hectare of vegetation located just to the east of Tower 65 of the new Cartago-San Isidro electrical transmission line. The burn area extends to the power lane that was cleared in 1983, and shrub stumps in the lane are charred, indicating that the fire postdated the cutting of the shrubs. It probably resulted from accidental or intentional ignition of the vegetation when the transmission tower and lines were installed in early 1984. Growth rings in stems of fire-killed *Vaccinium consanguineum* suggest that the vegetation was at least 16 years old at the time the fire occurred.

*Conejos site.* This burn site was located within the broad basin at the head of the glaciated valley known as the Valle de los Conejos in the Chirripó highlands (Fig. 2). The site lies on a south-facing slope between 3480 and 3500 m. The area last burned during the >5000 ha fire that swept through the highlands in March 1976 (Chaverri et al. 1976). At the time of the surveys the regenerating vegetation was nine years old. According to Weston (quoted in Kohkemper 1976), the Valle de los Conejos had previously burned in 1961, a date consistent with the maximum of fifteen rings found on fire-killed stems of *Vaccinium consanguineum*.

*Zacatales site.* The Zacatales site was located on the steep south-facing slope of Cerro Zacatales in the Buenavista highlands. Tran-





FIG. 2. General view of the head of the glaciated Valle de los Conejos, nine years after the major 1976 fire. The Conejos study site is visible in the background on the left side of the photograph. The peak in the center is Cerro Pirámide (3807 m). The dominant woody species is the dwarf bamboo *Swallenochloa subtessellata*.

sects were run between 3340 and 3370 m, within the same area sampled by Williamson et al. (1986) in 1982. Site visits showed that the fire, which appears to have covered about 10 ha, occurred between early February and late March of 1973 (Williamson et al. 1986). When surveyed in late 1984 and early 1985 the vegetation was about twelve years old. Fire-killed stems in two stages of decay were common at the site, indicating that the area had burned twice in recent decades. The more intact dead stems of *Vaccinium consanguineum* showed a maximum of twelve growth rings, suggesting that at the time of the 1973 fire the vegetation was at least this old. Older dead stems that had been killed by the next to last fire were too decayed to make reliable ring counts.

*Sábila site.* The Sábila site was located a few kilometers to the east of the Zacatales site on the southeastern face of Cerro Sábila. Elevations within the area sampled range from 3370 to 3410 m. Ring counts made in 1985 on regenerating *Vaccinium consanguineum* stems revealed a maximum of twelve rings, suggesting that the 15 ha fire occurred no later than 1973. The exact date of burning is



not known. I counted 29 growth rings on the largest dead stem of one regenerating *V. consanguineum*, suggesting that the vegetation was at least this old at the time of the last fire.

## RESULTS

*Postfire cover.* Table 2 shows cover data for the shrub and herb layers at the four páramo burn sites. The data are grouped together only to facilitate comparison; the arrangement is not meant to imply a successional sequence. Cover ranged from minimal at the Tower 65 site, where most of the ground was still bare one year after burning (Fig. 3), to nearly continuous after twelve years of regeneration at the Zacatales site. Patches of bare ground ranging in size from 0.1 to 0.5 m<sup>2</sup> were present at both the Conejos and Sábila sites, even in areas not shaded by the shrub canopy. Standing and downed fire-killed shrub and bamboo stems were conspicuous at all four sites (Fig. 4).

*Fire response.* Burning was complete or nearly so within all burn sites, and most plants had suffered total crown loss. The overall incidence of basal resprouting by the larger shrubs and bamboo ranged from 40% at the Zacatales site to 83% at the Conejos site, with differences largely attributable to variations in preburn species composition.

Chi-square tests indicated significant heterogeneity in fire responses (Table 3). The bamboo *Swallenochloa subtessellata* showed the highest resprout rate, with live shoots present within 99–100% of all burned clumps examined. Also exhibiting vigorous resprouting following burning were the common ericaceous shrubs *Vaccinium consanguineum* (90–98% resprout rate) and *Pernetia coriacea* (93–96% resprout rate). The shrub *Hypericum irazuense*, in contrast, suffered high mortality at the four sites; only 4–14% of burned individuals had suckered following burning. Also exhibiting low resprout success were the shrubs *Hypericum strictum* and *Senecio firmipes* (0 and 4%, respectively, with data only from the Tower 65 site). Low to intermediate frequencies of basal resprouting were shown by the shrubs *Rapanea pittieri* (15–25%) and *Escallonia poasana* (50–57%).

The association between prefire plant stature and fire response was tested using a median test (Sachs 1984). For each species, observations on prefire height (and, later, on prefire stem diameter) of both dead and resprouting plants were pooled together and ordered to determine the common median. The observations were then sorted according to whether they were larger or smaller than the common median, and a Fisher exact test (Sokal and Rohlf 1981) was applied to the resulting two-way table to test the null hypothesis that whether



TABLE 2. POSTFIRE VEGETATION COVER AT PARAMO BURN SITES. Only listed are species accounting for at least 1% of total shrub or herb layer cover at one of the sites. For data on rare species see Horn (1986). nr = not recorded in cover transects.

|   | Tower 65 site<br>1 yr after fire | Conejos site<br>9 yr after fire | Zacatales site<br>12 yr after fire | Sábila site<br>≥ 12 yr after fire |
|---|----------------------------------|---------------------------------|------------------------------------|-----------------------------------|
| Shrub layer   |                                  |                                 |                                    |                                   |
| <i>Swallenochloa subtessellata</i> (A. Hitchc.) McClure     | 5.5%                             | 31.8%                           | 2.9%                               | 34.7%                             |
| <i>Vaccinium consanguineum</i> Klotzsch                     | 3.0                              | 1.0                             | 5.1                                | 9.5                               |
| <i>Pernettia coriacea</i> Klotzsch                          | 2.0                              | 1.0                             | 17.1                               | 17.5                              |
| <i>Hypericum irazuense</i> Kuntze                           | <1                               | <1                              | 13.5                               | 2.5                               |
| <i>Escallonia poasana</i> J. D. Smith                       | nr                               | nr                              | 3.9                                | 3.3                               |
| <i>Castilleja talamancensis</i> N. Holmgren                 | <1                               | nr                              | 2.0                                | 1.2                               |
| <i>Hesperomeles heterophylla</i> (Ruíz Lopez & Pavón) Hook. | <1                               | <1                              | 1.0                                | 1.7                               |
| Cover of rare taxa (individually <1%)                       | 1.8                              | 1.0                             | 0.7                                | 2.4                               |
| Total cover, excluding overlap                              | 11.4%                            | 33.8%                           | 40.2%                              | 62.6%                             |
| Herb layer  |                                  |                                 |                                    |                                   |
| <i>Agrostis</i> sp.   | 2.2%                             | 3.2%                            | 12.9%                              | 3.0%                              |
| <i>Calamagrostis intermedia</i> (Presl) Steudel             | nr                               | nr                              | nr                                 | 2.8                               |
| <i>Calamagrostis</i> sp.                                    | nr                               | <1                              | 10.1                               | nr                                |
| <i>Muhlenbergia flabellata</i> Mez.                         | nr                               | 32.5                            | nr                                 | nr                                |
| Unidentified Gramineae                                      | 1.2                              | <1                              | <1                                 | 1.0                               |
| <i>Carex donnell-smithii</i> L. Bailey                      | nr                               | nr                              | nr                                 | 3.6                               |
| <i>Carex</i> sp.  | 1.5                              | 13.1                            | 13.4                               | nr                                |
| <i>Pernettia prostrata</i> (Cav.) Sleumer                   | 1.1                              | 4.5                             | 12.2                               | 2.8                               |
| <i>Valeriana prionophylla</i> Standley                      | nr                               | 2.1                             | <1                                 | nr                                |
| <i>Eryngium scaposum</i> Turcz.                             | nr                               | 1.1                             | <1                                 | nr                                |
| <i>Acaena cylindrostachya</i> Ruíz Lopez & Pavón            | <1                               | nr                              | 10.5                               | <1                                |
| <i>Alchemilla</i> sp.                                       | <1                               | <1                              | 7.6                                | 1.0                               |
| <i>Rubus eriocarpus</i> Liebm.                              | <1                               | nr                              | 2.1                                | <1                                |
| <i>Senecio oersterdianus</i> Benth.                         | nr                               | nr                              | 1.7                                | <1                                |
| <i>Lycopodium</i> sp.                                       | <1                               | nr                              | nr                                 | 1.5                               |
| Cover of rare taxa (individually <1%)                       | 2.7                              | 2.7                             | 3.6                                | 1.5                               |
| Total cover, excluding overlap                              | 8.7%                             | 59.0%                           | 70.4%                              | 17.2%                             |





FIG. 3. View within the Tower 65 burn site one year after the fire. Large dead shrub in the center of the photograph is *Hypericum irazuense*; regenerating clumps of the bamboo *Swallenochloa subtessellata* and resprouting shrubs of *Vaccinium consanguineum* and *Pernetia coriacea* surround the dead plant. The herb in the right foreground is *Senecio oerstedianus*. Note the abundance of standing dead wood and the extent of bare ground.



a shrub's prefire height or stem diameter fell above or below the median was unrelated to its survival.

The median tests revealed little association between fire response and either prefire height or stem diameter for the most common shrubs. At the Tower 65 site there were more small-diameter *Rapanea pittieri* in the "dead" category and more large-diameter *R. pittieri* in the "resprouter" category than would be expected under the null hypothesis of no association ( $p = 0.026$ ), suggesting that larger diameter individuals were more likely to resprout than smaller diameter individuals. No association was apparent between prefire height and fire response. At the Sábila site, taller stems were associated with higher survival for *Hypericum irazuense* ( $p = 0.03$ ), but the large number of broken stems that had to be excluded from calculations makes the finding suspect. Prefire stem diameter and fire response were not significantly associated.

At the Sábila site the fire response of *Escallonia poasana* was significantly associated with both prefire height and prefire stem diameter. Larger plants were more often in the "dead" category and smaller plants were more often in the "resprouter" category than would be expected if no association existed ( $p = 0.05$  for stem height,  $p = 0.002$  for stem diameter), suggesting that smaller plants were more likely to resprout after burning than larger plants.

Few postfire shrub colonists other than *Hypericum irazuense* were observed at the sites. Abundant *H. irazuense* recruitment (all from seed) was observed at the Zacatales and Sábila sites (Fig. 5), but had not occurred at the younger burn sites. Seedling establishment by associated woody species was rarely observed. The common ericaceous shrubs *Vaccinium consanguineum* and *Pernetia coriacea*, and the bamboo *Swallenochloa subtessellata* produce widely diverging roots and rhizomes, and most postfire colonists probably represented sprouts produced at new points along pre-existing root/rhizome networks rather than new genetic individuals established from seed.

*Changes in species composition.* The varying rates of shrub and bamboo mortality and seedling establishment at the four burn sites led to changes in species composition (Fig. 6). Most notable was the marked reduction in the density of *Hypericum irazuense* at the Tower 65 and Conejos sites. The narrow-leaved congener *Hypericum strictum* also showed a marked decline in density at the Tower 65 site, where no resprouting individuals and no seedlings were observed one year after burning.

*Postfire growth rates.* Table 4 gives prefire and postfire heights for the bamboo *Swallenochloa subtessellata* and its five most common shrub associates. Among these species *Swallenochloa* consistently showed the highest postfire growth rate. Prior to the fires the bamboo





FIG. 4. View within the Sábila burn site. Note the abundance of standing dead wood and the presence of bare patches of ground twelve or more years after burning.

averaged between one and two meters in height, with the tallest plants at the Tower 65 site and the smallest at the Conejos site. Height recovery was 18% one year after burning at the Tower 65 site; 98% nine years after burning at the Conejos site; 113% twelve years after burning at the Zacatales site; and 129% twelve or more years after burning at the Sábila site. At the Tower 65 site, the tender new shoots of the bamboo had been grazed by native rabbits (*Silvilagus* sp.) and by at least one cow, such that the data in Table 4 may underestimate the actual first year growth increment of the plant. Little or no evidence of grazing was apparent at the older burn sites, but may have occurred in the past. Grazing damage on plants other than *Swallenochloa subtessellata* was rarely observed.

Prior to burning, the ericaceous shrub *Vaccinium consanguineum* averaged around a meter in height. Percentage height recovery was 26% at the Tower 65 site, 71% at the Conejos site, 87% at the Zacatales site, and 88% at the Sábila site. The more prostrate ericaceous shrub *Pernetia coriacea* showed percentage height recovery of 24% at the Tower 65 site, 97% at the Zacatales site, and 79% at the Sábila site.



TABLE 3. FIRE RESPONSES OF WOODY SPECIES AT PARAMO BURN SITES. Table includes only species with a sample size greater than 20 at individual sites. Chi-square statistic indicates heterogeneity of fire responses. Abbreviations in brackets are used for the taxa in Figure 6.

|   |                   |            |                   |                   |
|---|-------------------|------------|-------------------|-------------------|
| Tower 65 site   |                   |            |                   |                   |
| Species   | Response category |            |                   |                   |
|   | Dead              | Resprouter | Fire survivor     |                   |
| <i>Swallenochloa subtessellata</i> [Ss]                         | 0                 | 68         | 3                 |                   |
| <i>Vaccinium consanguineum</i> [Vc]                             | 2                 | 113        | 10                |                   |
| <i>Pernettia coriacea</i> [Pc]                                  | 7                 | 88         | 15                |                   |
| <i>Hypericum irazuense</i> [Hi]                                 | 100               | 4          | 15                |                   |
| <i>Hypericum strictum</i> Kunth [Hs]                            | 51                | 0          | 11                |                   |
| <i>Senecio firmipes</i> Greenman [Sf]                           | 22                | 1          | 0                 |                   |
| <i>Rapanea pittieri</i> Mez [Rp]                                | 12                | 4          | 5                 |                   |
| $\chi^2 = 419, df = 12, p < 0.001.$                             |                   |            |                   |                   |
| Conejos site  |                   |            |                   |                   |
| Species   | Response category |            |                   |                   |
|   | Dead              | Resprouter | Postfire colonist |                   |
| <i>Swallenochloa subtessellata</i> [Ss]                         | 5                 | 386        | 4                 |                   |
| <i>Vaccinium consanguineum</i> [Vc]                             | 2                 | 19         | 5                 |                   |
| <i>Hypericum irazuense</i> [Hi]                                 | 80                | 5          | 1                 |                   |
| $\chi^2 = 463, df = 4, p < 0.001.$                              |                   |            |                   |                   |
| Zacatales site  |                   |            |                   |                   |
| Species   | Response category |            |                   |                   |
|   | Dead              | Resprouter | Fire survivor     | Postfire colonist |
| <i>Vaccinium consanguineum</i> [Vc]                             | 2                 | 48         | 10                | 15                |
| <i>Pernettia coriacea</i> [Pc]                                  | 3                 | 72         | 14                | 22                |
| <i>Hypericum irazuense</i> [Hi]                                 | 240               | 34         | 43                | 434               |
| $\chi^2 = 429, df = 6, p < 0.001.$                              |                   |            |                   |                   |
| Sábila site   |                   |            |                   |                   |
| Species   | Response category |            |                   |                   |
|   | Dead              | Resprouter | Fire survivor     | Postfire colonist |
| <i>Swallenochloa subtessellata</i> [Ss]                         | 0                 | 41         | 0                 | 8                 |
| <i>Vaccinium consanguineum</i> [Vc]                             | 1                 | 65         | 2                 | 6                 |
| <i>Pernettia coriacea</i> [Pc]                                  | 5                 | 100        | 4                 | 15                |
| <i>Hypericum irazuense</i> [Hi]                                 | 147               | 23         | 13                | 98                |
| <i>Rapanea pittieri</i> [Rp]                                    | 17                | 3          | 1                 | 2                 |
| <i>Escallonia poasana</i> [Ep]                                  | 9                 | 12         | 0                 | 1                 |
| $\chi^2$ statistic cannot be calculated due to low cell counts. |                   |            |                   |                   |





FIG. 5. Seedlings of *Hypericum irazuense* growing up amidst shrubs of the same species killed by fire twelve years earlier at the Zacatales site. Cerro Zacatales (3399 m) is visible in the background. The stick is one meter long.

The shrub *Hypericum irazuense* averaged 90–160 cm tall at the time of the four fires investigated; percentage height recovery for the rare individuals that resprouted was 15% at the Tower 65 site, 64% at the Conejos site, 71% at the Zacatales site, and 70% at the Sábila site. *Hypericum irazuense* seedlings at the latter two sites were



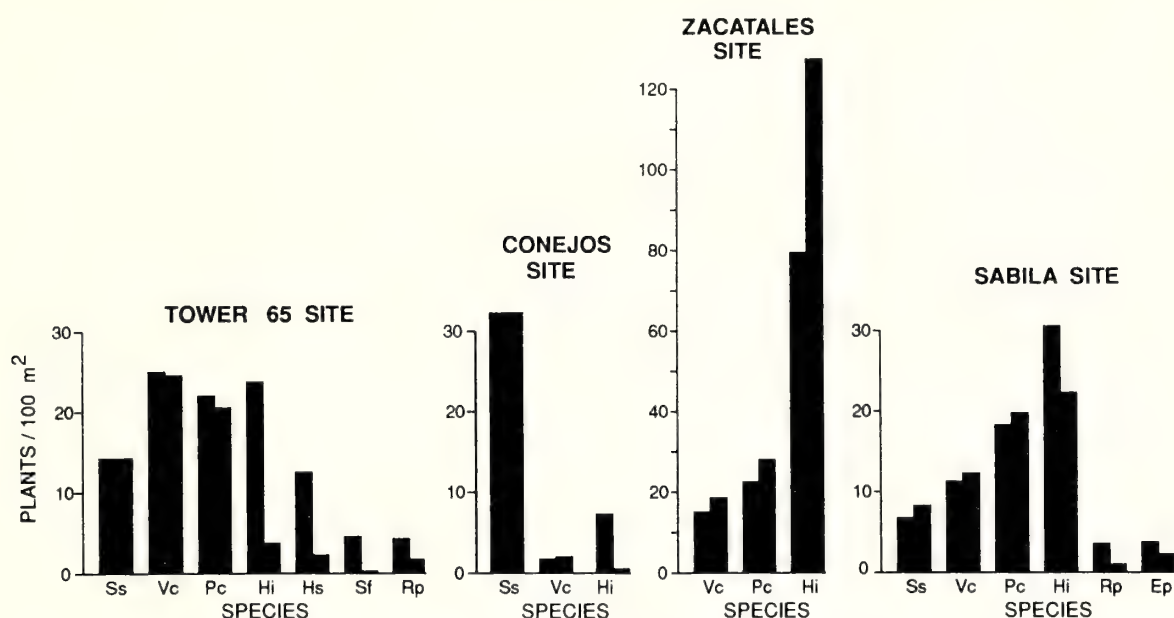


FIG. 6. Prefire (first bar) and postfire (second bar) density of common shrubs and bamboo at the burn sites. See Table 3 for key to species abbreviations. Note change of scale for the Zacatales data.

about 10% smaller on average than resprouts. Height recovery by resprouting shrubs of *Rapanea pittieri* and *Escallonia poasana* at the older burn sites was faster on both an absolute and percentage basis; both plants had more than regained their prefire stature at the Sábila site and *Escallonia* had also exceeded its average prefire size at the Zacatales site.

## DISCUSSION

The slow rates of postfire vegetation recovery and litter breakdown documented at the burn sites are consistent with observations made by Janzen (1973a) following a 1969 fire on Cerro Asunción. Three years after the Asunción fire, Janzen found that there were still large areas of uncolonized ground, and that most of the shrub stems killed by the fire were still intact and standing. Surveys at the Conejos, Zacatales, and Sábila sites revealed that bare patches of ground and upright fire-killed stems can persist for nine or more years following burning. The slow rates of growth and colonization that characterize these tropical high montane environments stand in marked contrast to the usual situation in the lowland tropics, where fire-killed wood decomposes quickly, and openings are rapidly colonized by dense stands of sucker sprouts and the seedlings of fast growing, weedy secondary species (Janzen 1973a).

Patterns of postfire vegetation development in the Talamancan páramos support the initial floristics model of succession (Egler 1954). Following disturbance, most páramo shrubs and bamboo replace themselves directly, usually by resprouting from protected buds. Woody perennials comprising the mature vegetation are present in



TABLE 4. PREFIRE AND POSTFIRE HEIGHTS OF RESPROUTING SHRUBS AND BAMBOO AT PARAMO BURN SITES. Values listed are means, (sample sizes), and standard deviations. Sample sizes for prefire heights are smaller than those for postfire heights because of the exclusion of broken dead stems from the calculations. This table shows only data for the six most common woody species. For data on prefire stature of dead plants, and postfire stature of fire-surviving plants and postfire colonists see Horn (1986).

| Species                           | Height (cm) at Tower 65 site<br>1 year after burning |                       | Height (cm) at Conejos site<br>9 years after burning |                       |
|-----------------------------------|--|-----------------------|--|-----------------------|
|                                   | Prefire  | Postfire              | Prefire  | Postfire              |
| <i>Swallenochloa subtesellata</i> | 186.2 (65)<br>SD 54.4                                | 34.4 (68)<br>SD 17.4  | 104.6 (100)<br>SD 39.3                               | 102.8 (91)<br>SD 45.8 |
| <i>Vaccinium consanguineum</i>    | 83.5 (103)<br>SD 37.5                                | 21.7 (103)<br>SD 11.5 | 107.1 (17)<br>SD 51.9                                | 75.6 (18)<br>SD 25.8  |
| <i>Pernetia coriacea</i>          | 67.4 (87)<br>SD 24.6                                 | 16.3 (88)<br>SD 5.3   |  |                       |
| <i>Hypericum irazuense</i>        | 129.8 (4)<br>SD 60.1                                 | 20.0 (4)<br>SD 18.7   | 143.0 (4)<br>SD 43.8                                 | 91.0 (4)<br>SD 44.9   |
| <i>Rapanea pittieri</i>           | 131.3 (4)<br>SD 60.2                                 | 19.0 (4)<br>SD 18.7   |  |                       |
| <i>Escallonia poasana</i>         | 84 (1)   | 14 (1)                |  |                       |

| Species                           | Height (cm) at Zacatales site<br>12 years after burning |                       | Height (cm) at Sábila site<br>≥ 12 years after burning |                       |
|-----------------------------------|---|-----------------------|--|-----------------------|
|                                   | Prefire   | Postfire              | Prefire  | Postfire              |
| <i>Swallenochloa subtesellata</i> | 124.9 (11)<br>SD 51.6                                   | 140.9 (14)<br>SD 64.8 | 147.8 (28)<br>SD 47.0                                  | 190.6 (41)<br>SD 52.8 |
| <i>Vaccinium consanguineum</i>    | 76.7 (157)<br>SD 34.7                                   | 66.7 (167)<br>SD 20.7 | 116.6 (52)<br>SD 46.4                                  | 103.0 (65)<br>SD 35.3 |
| <i>Perettia coriacea</i>          | 46.9 (104)<br>SD 12.7                                   | 45.7 (134)<br>SD 11.4 | 82.4 (52)<br>SD 31.8                                   | 65.0 (100)<br>SD 25.4 |
| <i>Hypericum irazuense</i>        | 91.1 (28)<br>SD 29.9                                    | 65.1 (78)<br>SD 23.2  | 159.4 (7)<br>SD 29.9                                   | 110.9 (23)<br>SD 46.7 |
| <i>Rapanea pittieri</i>           | 148.5 (2)<br>SD 2.1                                     | 116.5 (2)<br>SD 19.1  | 137.0 (2)<br>SD 5.7                                    | 172.0 (3)<br>SD 61.2  |
| <i>Escallonia poasana</i>         | 83.2 (21)<br>SD 34.1                                    | 96.3 (30)<br>SD 39.4  | 86.7 (6)<br>SD 40.5                                    | 148.3 (12)<br>SD 43.6 |

the burn site the first year after fire, and limited colonization by other species takes place once the first year population is established.

*Basal resprouting by shrubs and bamboo.* The fire response data confirm and extend the results of Williamson et al. (1986), who reported that over 90% of the ericaceous shrubs on Cerro Zacatales had resprouted following burning, as compared to only 11% of *Hypericum irazuense* shrubs. Patterns described here differ markedly, however, from the trends evident following the 1969 Asunción fire studied by Janzen (1973a). Postfire vegetation development at Cerro



Asunción was characterized by abundant regeneration of *Hypericum irazuense* (Janzen's *Hypericum caracasenum*) following crown loss. Williamson et al. (1986) contrasted the fire response of *H. irazuense* at the Asunción and Zacatales sites, and suggested that the higher mortality at Cerro Zacatales was due to the depletion of root reserves by successive fires. While there is evidence of more frequent burning at the Zacatales site, the discovery of high *Hypericum irazuense* mortality on Cerro Sábila, where recent fire recurrence intervals appear similar to those at Janzen's Asunción site, suggests that other environmental conditions, such as perhaps soil moisture conditions at the time of the fire, may explain the much higher resprout success at the Asunción site.

The near elimination of the bamboo *Swallenochloa subtesellata* from the Zacatales site was cited by Williamson et al. (1986) as a second consequence of repeated burning. This interpretation contradicts my data from the site, which showed little evidence of *Swallenochloa* mortality, and is at variance with the results from the other burn sites, where vigorous postfire sprouting by the bamboo has allowed it to maintain or even increase its dominance. I doubt that the recent (post-1950) fire recurrence interval at the site (estimated by Williamson and associates to be on the order of ten years) has been too short for between-fire recovery of root reserves, because at higher elevations in the Chirripó massif bamboo clumps that burned in 1976 and again in 1982 have produced abundant resprouts (Horn unpubl. data). If *Swallenochloa* was once more important at the Zacatales site, factors other than fire were probably responsible for its decline.

Gill (1981) has discussed the possible importance of the prefire age of a plant in determining its regenerative capacity following crown loss. Although higher survival might be expected among larger (and presumably older) plants with well-developed root reserves, median tests revealed no consistent associations between the size of páramo shrubs and their resprout success. For the shrub *Escallonia poasana*, susceptibility to fire seems to increase with size. Higher fire mortality among older shrubs has been reported by Stohlgren (1985) for *Adenostoma fasciculatum* H. & A. in the California chaparral. Stohlgren suggested that the older shrubs may contain more dead wood from previous fires, and that this might have made them more likely to be killed by fire. This explanation would not apply at the Sábila site, however, because the large individuals of *Escallonia poasana* killed by the fire showed no evidence of having burned previously.

*Growth and recovery of resprouting shrubs and bamboo.* The data on shrub and bamboo heights summarized in Table 4 and by Janzen (1973a) and Williamson et al. (1986) suggest that the growth of



woody perennials is most rapid during the first few years after burning. The higher initial growth rates may in part reflect improved soil fertility following the release of nutrients by burning.

The consistently greater heights of shoots of *Swallenochloa subtessellata* as compared to those of the common woody dicots confirm Janzen's (1983) statement that the bamboo exhibits one of the fastest rates of regrowth in páramo vegetation. It is worth stressing, however, that on an absolute basis the growth of the bamboo is quite slow; the field data support Janzen's (1983) observation that about 8–10 years are required for burned plants to regain their prefire adult statures. Associated woody dicots may require a decade or more to reach their prefire adult size of 1–2 m. Measurements of stem diameters (reported in Horn 1986) indicate that for all species except *Escallonia poasana*, the recovery of basal stem diameter lags far behind height recovery.

Páramo regeneration, while slow in comparison to regeneration in lowland tropical forests, proceeds at rates comparable to those measured in tropical montane forests in Costa Rica and Puerto Rico. Ewel (1980) artificially cleared montane rain forest from eight plots near Ojo de Agua (3000 m) in the Cordillera de Talamanca to monitor regrowth; after one year the average height of the three tallest plants was only 70 cm. One year after burning at the Tower 65 site the three tallest plants (all clumps of *Swallenochloa subtessellata*) averaged 85 cm in height. Byer and Weaver (1977) noted similarly slow rates of growth on artificial clearings within elfin woodland in the Luquillo mountains of Puerto Rico. One year after clearing, the mean maximum heights for woody sprouts in three clearings was 33.6 cm, a value quite close to the mean maximum height of 34.4 cm for *Swallenochloa subtessellata* at Tower 65.

Postfire regeneration at the Tower 65 site occurred more slowly than it did following a fire in a montane mire (elev. 2690 m) near Tres de Junio in the Cordillera de Talamanca (Horn 1989b). In one year of growth the fastest growing shrub in the mire, *Hesperomeles heterophylla*, had produced resprouts averaging 68 cm in height, or about twice the mean height of the highest culms of *Swallenochloa subtessellata* at Tower 65.

*Shrub and herb colonization.* The long persistence of bare patches of ground within the study burns reflects both the slow production and growth of new shoots from surviving rootstocks and an extremely low rate of seedling colonization. The observed paucity of herb or shrub seedlings one year after the Tower 65 fire, and their rarity three years after the Asunción fire (Janzen 1973a), suggests that soil seed pools are small or that seeds suffer high mortality from fire. Unlike fire-prone shrub communities in the mediterranean-climate regions, the Talamancan páramos do not harbor a dormant



seed bank of herbaceous species that proliferate following burning. The páramo shrubs and bamboo similarly show little reliance on either in-soil seed storage or fire-stimulated germination. Instead, postfire seedling colonization by woody perennials depends on seed production by plants that survived the fire, or on the influx of seeds from plants in surrounding, unburned areas. In some cases, seedling colonization may not occur until plants that regenerated after the fire from basal buds reach maturity and begin seed production within the burn site.

The dominance of tussock grasses and sedges in the postburn herbaceous cover may be due primarily to the ability of these plants to survive fires, rather than to an ability to recolonize burned areas as seedlings. The perennating buds of these graminoids are generally protected from fire by their position underground or within persistent leaf bases, and many of the plants are able to resprout rapidly after burning. Chaverri et al. (1976) noted that burned sedges within the Chirripó páramo had produced sprouts up to 15 cm long within one month of the 1976 fire. Among herbaceous and semi-woody dicots, *Castilleja talamancensis*, *Rubus eriocarpus*, and *Acaena cylindrostachya* also resprout vigorously following burning, and their importance in the herbaceous cover at recent burn sites is probably due as much to fire survival as to postfire seedling establishment.

Among the woody perennials at the burn sites only *Hypericum irazuense* had established abundant seedlings. Twelve years after the last fire at the Zacatales site, seedling recruitment had more than compensated for the heavy fire-induced mortality of this species. Most of the seedlings were closely spaced, however, and natural thinning may reduce their density. Williamson et al. (1986) tallied few seedlings over 40 cm high in their 1982 survey at the site; they reported that most of the *Hypericum* recruits seen were only 10–25 cm high. That most of the seedlings were at least twice this high in 1985 suggests that the plants observed by Williamson and associates had only recently become established, and hence that the biggest pulse of seedling establishment did not occur until several years after the 1973 fire.

Substantial *Hypericum irazuense* recruitment was also apparent at the Sábila burn site, but had not occurred at the Conejos site. This presumably reflects the very large size of the 1976 Chirripó fire and the shortage of flowering plants to reseed the burn site. If repopulation of burned areas by *H. irazuense* depends primarily on seed influx from adjacent, unburned vegetation, the rate of seedling colonization should be lower the larger the fire and the more complete the burn.

The near complete reliance on vegetative regeneration by the common woody perennials in the Costa Rican páramos means that openings created by fire are slow to be colonized. Even the prolific



resprouter *Swallenochloa subtessellata* seems incapable of rapid spread. Nearly all of the bamboo clumps in the burn sites contained charred culms, indicating that they had been present prior to the fires. Some of the clumps had enlarged following burning by sprouting from lateral positions within the clumps. A few plants had become established after the fires, probably through the production of shoots at more distant points along extensive, preexisting networks of rhizomes. But even at the older sites, the bamboo had not yet spread into many of the gaps created by burning.

The relatively poor colonizing ability of *Swallenochloa subtessellata* is due largely to the fact that the species rarely sets seed. Although it is always possible to find some plants in flower, the grass specialist Richard Pohl (1980) reported that he has never detected filled caryopses in herbarium specimens, nor observed seedlings in the field. Janzen (1983) has suggested that this may reflect a pollen shortage among plants flowering out of phase with the rest of a gregariously flowering population. Low pollen viability may also contribute to the low seed set. Pollen grains in anthers taken from two specimens in the University of California, Berkeley, herbarium (UC 1434192, UC M111383) were misshapen and did not stain in lactophenol cotton blue, indicating that at the time the plants were pressed the pollen grains contained no protoplasm. The possibility that existing populations of *Swallenochloa subtessellata* in the Costa Rican páramos are male sterile deserves further attention.

*Regenerative strategies and postfire vegetation change.* The reproductive modes of the common woody perennials in the Costa Rican páramos resemble the regenerative strategies identified by Zedler et al. (1983) in fire-prone chaparral shrublands in California. The bamboo *Swallenochloa subtessellata* and the ericaceous shrubs *Vaccinium consanguineum* and *Pernetia coriacea* exemplify the "sprouter-nonseeder" mode: most burned plants survive the fire by resprouting from the base, but few or no seedlings are produced. The shrub *Hypericum irazuense* follows the "sprouter-seeder" pattern: the shrub resprouts infrequently, but supplements vegetative regeneration with more abundant seedling recruitment. However, the stored seed reserves and fire-stimulated germination that makes this strategy so effective in chaparral communities seem to be lacking in the páramos. Insufficient data are available to characterize the reproductive behavior of the less common páramo shrubs, but most appear to rely heavily on vegetative reproduction. The shrub *Hypericum strictum* suffered complete mortality at the only site where it was common (Tower 65), and may be an obligate seeder.

The data from the four páramo burn sites indicate that the more fire-resistant sprouters are clearly favored in the first 5–10 years after burning. The apparent absence of in-soil seed storage puts the fire-



sensitive species *Hypericum irazuense* at a distinct disadvantage during the first several postfire years. Delayed seedling recruitment may in time compensate for heavy fire-induced mortality, but a fire-free interval of at least two decades will likely be required for recruits to obtain statures comparable to those of the fire-killed plants they have replaced.

#### ACKNOWLEDGMENTS

I thank Roger Horn for field assistance, and Daniel Janzen, Jon Keeley, and Richard Corlett for critical reviews of the manuscript. Roger Byrne, Herbert Baker, Theodore Oberlander, and James Parsons provided helpful comments on an earlier version of this paper. Funding was provided by the Institute of International Education, the Association of American Geographers, and the Center for Latin American Studies of the University of California, Berkeley.

#### LITERATURE CITED

- BAUER, H. L. 1943. The statistical analysis of chaparral and other plant communities by means of transect samples. *Ecology* 21:45–60.
- BYER, M. D. and P. L. WEAVER. 1977. Early secondary succession in an elfin woodland in the Luquillo mountains of Puerto Rico. *Biotropica* 9:35–47.
- CHAVERRI, A., C. VAUGHAN, and L. J. POVEDA. 1976. Informe de la gira efectuada al macizo de Chirripó al raíz del fuego ocurrido en Marzo de 1976. *Revista de Costa Rica* 11:243–279.
- CUATRECASAS, J. 1979. Comparación fitogeográfica de páramos entre varias cordilleras. Pp. 89–99 in M. L. Salgado-Labouriau (ed.), *El medio ambiente páramo*. Ediciones Centro de Estudios Avanzados, Mérida, Venezuela.
- EGLER, F. 1954. Vegetation science concepts. I. Initial floristic composition, a factor in old-field vegetation development. *Vegetatio* 14:412–417.
- EWEL, J. 1980. Tropical succession: manifold routes to maturity. *Tropical Succession* (Supplement to *Biotropica* 12):2–7.
- GILL, A. M. 1981. Fire adaptive traits of vascular plants. Pp. 208–230 in H. A. Mooney et al. (tech. coords.), *Fire regimes and ecosystem properties*. U.S. Dept. of Agriculture Forest Service General Technical Report WO-26.
- GRUBB, P. J. 1970. The impact of man on the páramo of Cerro Antisana, Ecuador. *J. Applied Ecol.* 7(2):7P–8P.
- HARTSHORN, G. S. 1983. Plants: introduction. Pp. 118–157 in D. H. Janzen (ed.), *Costa Rican natural history*. Univ. Chicago Press, Chicago.
- HASTENRATH, S. 1963. Zumeinflub der massenerhebung auf den verlauf der klima- und vegetationstufen in Mittelamerika und im sudlichen Mexico. *Geogr. Ann.* 45:76–83.
- . 1973. On the Pleistocene glaciation of the Cordillera de Talamanca, Costa Rica. *Z. Gletscherkd.* 9:105–121.
- HORN, S. P. 1986. Fire and páramo vegetation in the Cordillera de Talamanca, Costa Rica. Ph.D. dissertation. Univ. California, Berkeley.
- . 1989a. Prehistoric fires in the Chirripó highlands of Costa Rica: sedimentary charcoal evidence. *Revista de Biología Tropical* (in press).
- . 1989b. Effect of burning on a montane mire in the Cordillera de Talamanca, Costa Rica. *Brenesia* (in press).
- JANZEN, D. H. 1973a. Rate of regeneration after a tropical high elevation fire. *Biotropica* 5:117–122.
- . 1973b. Sweep samples of tropical foliage insects: descriptions of study sites, with data on species abundances and size distributions. *Ecology* 54:659–678.



- . 1983. *Swallenochloa subtessellata* (chusquea, batamba, matamba). Pp. 330–331 in D. H. Janzen (ed.), *Costa Rican natural history*. Univ. Chicago Press, Chicago.
- KOHKEMPER M., M. 1976. Sexta expedición al macizo del Chirripó. Instituto Geográfico Nacional de Costa Rica. Informe Semestral Enero-Junio:63–69.
- LAUER, W. 1981. Ecoclimatological conditions of the páramo belt in the tropical high mountains. *Mountain Res. Develop.* 1:209–221.
- OTAROLA D., C. E. 1976. Caracterización y clasificación de algunos suelos de la Cordillera de Talamanca. Thesis. Universidad de Costa Rica. San José, Costa Rica.
- POHL, R. 1980. Flora costaricensis: family number 15, Gramineae. *Fieldiana, Bot.*, n.s. 4:1–608.
- SACHS, L. 1984. *Applied statistics: a handbook of techniques*, 2nd ed. Springer-Verlag, New York.
- SMITH, A. P. 1981. Growth and population dynamics of *Espletia* (Compositae) in the Venezuelan Andes. *Smithsonian Contrib. Bot.* 48:1–45.
- SOKAL, R. R. and F. J. ROHLF. 1981. *Biometry*, 2nd ed. W. H. Freeman and Company, San Francisco.
- STOHLGREN, T. J. 1985. Fire-caused mortality in chamise chaparral. Pp. 385–387 in J. E. Lotan et al. (tech. coords.), *Proceedings—symposium and workshop on wilderness fire*. U.S. Dept. of Agriculture Forest Service General Technical Report INT-182.
- WEBER, H. 1959. Los páramos de Costa Rica y su concatenación fitogeográfica con los andes suramericanos. Instituto Geográfico Nacional, San José, Costa Rica.
- WEYL, R. 1957. Contribución a la geología de la Cordillera de Talamanca de Costa Rica (Centro America). Instituto Geográfico Nacional, San José, Costa Rica.
- WILLIAMSON, G. B., G. E. SCHATZ, A. ALVARADO, C. S. REDHEAD, A. C. STAM, and R. W. STERNER. 1986. Effects of repeated fires on tropical páramo vegetation. *Trop. Ecol.* 27:62–69.
- WORLD METEOROLOGICAL ORGANIZATION. 1953. World distribution of thunderstorm days. I. Tables. World Meteorological Organization, Geneva.
- . 1956. World distribution of thunderstorm days. II. Tables of marine data and world maps. World Meteorological Organization, Geneva.
- ZEDLER, P. H., C. R. GAUTIER, and G. S. McMASTER. 1983. Vegetation response to extreme events: the effect of a short interval between fires in California chaparral and coastal scrub. *Ecology* 64:809–818.

(Received 25 Aug 1988; revision accepted 24 Jan 1989.)



A NEW SPECIES OF *ERIGERON* (ASTERACEAE: ASTEREAEE)  
FROM CENTRAL NEW MEXICO

RICHARD SPELLENBERG

Department of Biology, New Mexico State University,  
Las Cruces, NM 88003-0001

PAUL KNIGHT

State Forestry, Energy, Minerals, and  
Natural Resources Department,  
Villagra Building, Santa Fe, NM 87503

ABSTRACT

*Erigeron acomanus* is an inhabitant of sandy slopes beneath sandstone cliffs in central New Mexico. It is morphologically similar to *E. tener* of the Intermountain Region of the western United States. *Erigeron acomanus* has 16–30 white rays, has 4–10 leaves on the flowering stem, and forms leafy mats 10–70 cm in diameter. Pappus bristles are 20–25 in number and are about the length of the disk corolla. *Erigeron acomanus* lacks the peg-like glandular hairs present on the stems of *E. tener*.

Since the passage of the Endangered Species Act of 1973, each of us has been involved in numerous surveys to determine the presence of endangered or threatened plant species on lands in New Mexico administered by federal land management agencies. On two such surveys, at separate locations, we independently discovered an *Erigeron* in central New Mexico that could not be identified in local keys (e.g., Martin and Hutchins 1981) or Cronquist's (1947) revision of the genus. Morphologically it most closely resembles *E. tener* (A. Gray) A. Gray, a widespread species from the Intermountain Region, but *E. acomanus* is readily recognized by several morphological features. It is also disjunct from *E. tener* by more than 500 km (Fig. 1). We describe it here as a new species.

***Erigeron acomanus* Spellenberg and Knight, sp. nov.** (Fig. 2). — TYPE: USA, New Mexico, McKinley Co., ca. 3.2 km N of Prewitt at base of cliffs in canyon, T14N R12W sect. 24 NW ¼ of NE ¼, 35°26'03"N, 108°03',29"W, elev. 2120 m, 14 Jul 1983, *Knight* 2689 (holotype, UC; isotypes; ARIZ, ASU, COLO, NMC, NY, RM, TEX, UNM, US).

Plantae perennes rosulis foliaceis, tegetes 10–70 mm diametrum formantes. Laminae foliorum oblanceolatae vel spathulatae, 8–23 mm longae, 2–7 mm latae, pubescentiae modice in superficiebus ambabus, laminae ad basim in petiola sensim attenuatae. Caules



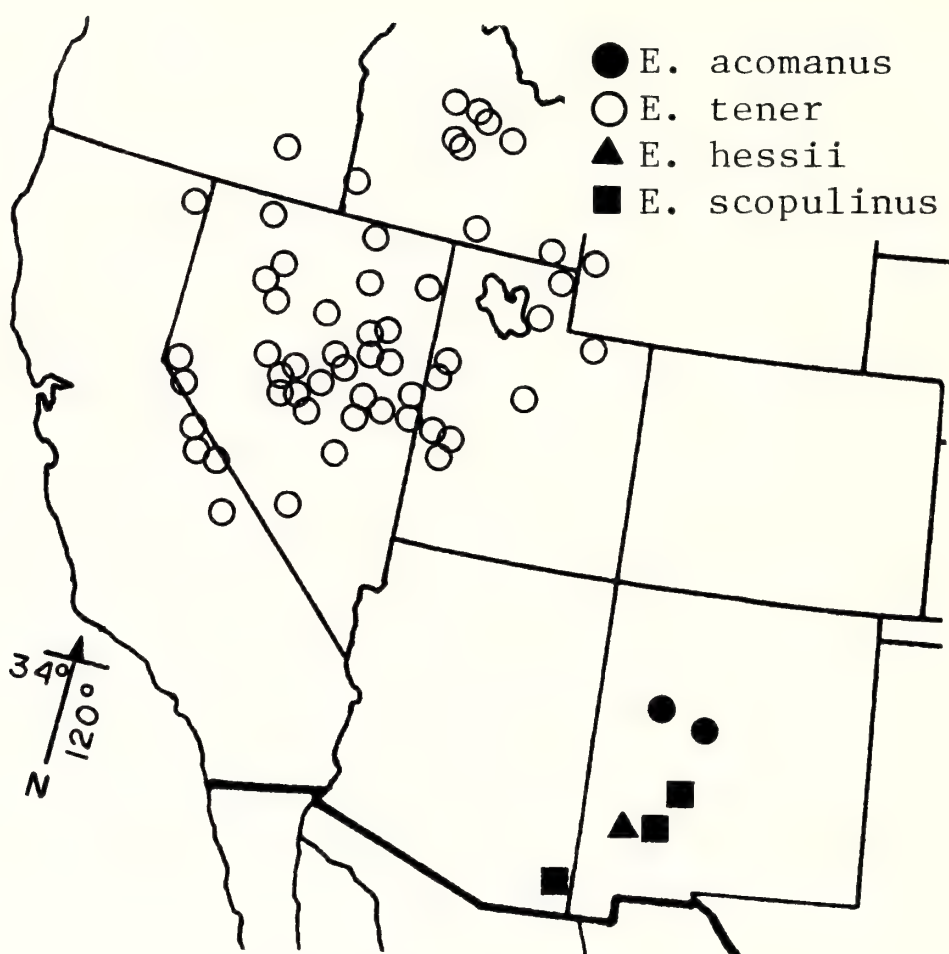


FIG. 1. Western United States showing distribution of *Erigeron acomanus*, *E. tener*, *E. hessii*, and *E. scopulinus*.

4.5–15 cm alti, 4–10 folia et 1 capitulum ferentes. Capitula 8–10 mm diametro, ca. 5 mm alta. Ligulae 16–30, albae, 4.5–9 mm longae, 1.3–1.8 mm latae. Setae pappi 20–25, 1.5–2.5 mm longae. Chromosomatum gametophytorum numerus 9.

Taprooted perennial forming a mat 10–70 cm in diameter, the caudex branches covered by persistent leaf bases. Leaves mostly basal, spreading or ascending, 8–30 in rosettes at ends of caudex branches; blades oblanceolate to narrowly obovate or spatulate, 8–23 mm long, 2–7 mm wide, round or obtuse at the tip, evenly tapered to a petiole-like base 3–13 mm long, moderately puberulent on both surfaces with fine, appressed, slightly wavy hairs ca. 0.3 mm long, the leaves on the flowering stem similar but becoming progressively smaller toward the capitulum. Flowering stems erect, 4.5–15 cm tall, bearing 4–10 leaves. Capitula solitary, pendulous in bud, erect in flower and fruit. Flowering stem strigose, usually with a single bract-like leaf about the length of the phyllaries immediately beneath the involucre, this separate from the next leaf on the stem by a space of 2–15 mm. Involucre ca. 5 mm high, 7–10 mm across (when pressed). Phyllaries 25–38, lanceolate, 2.5–4 mm long, 0.5–0.8 mm wide, purplish especially on the margins, greenish on the back, glan-



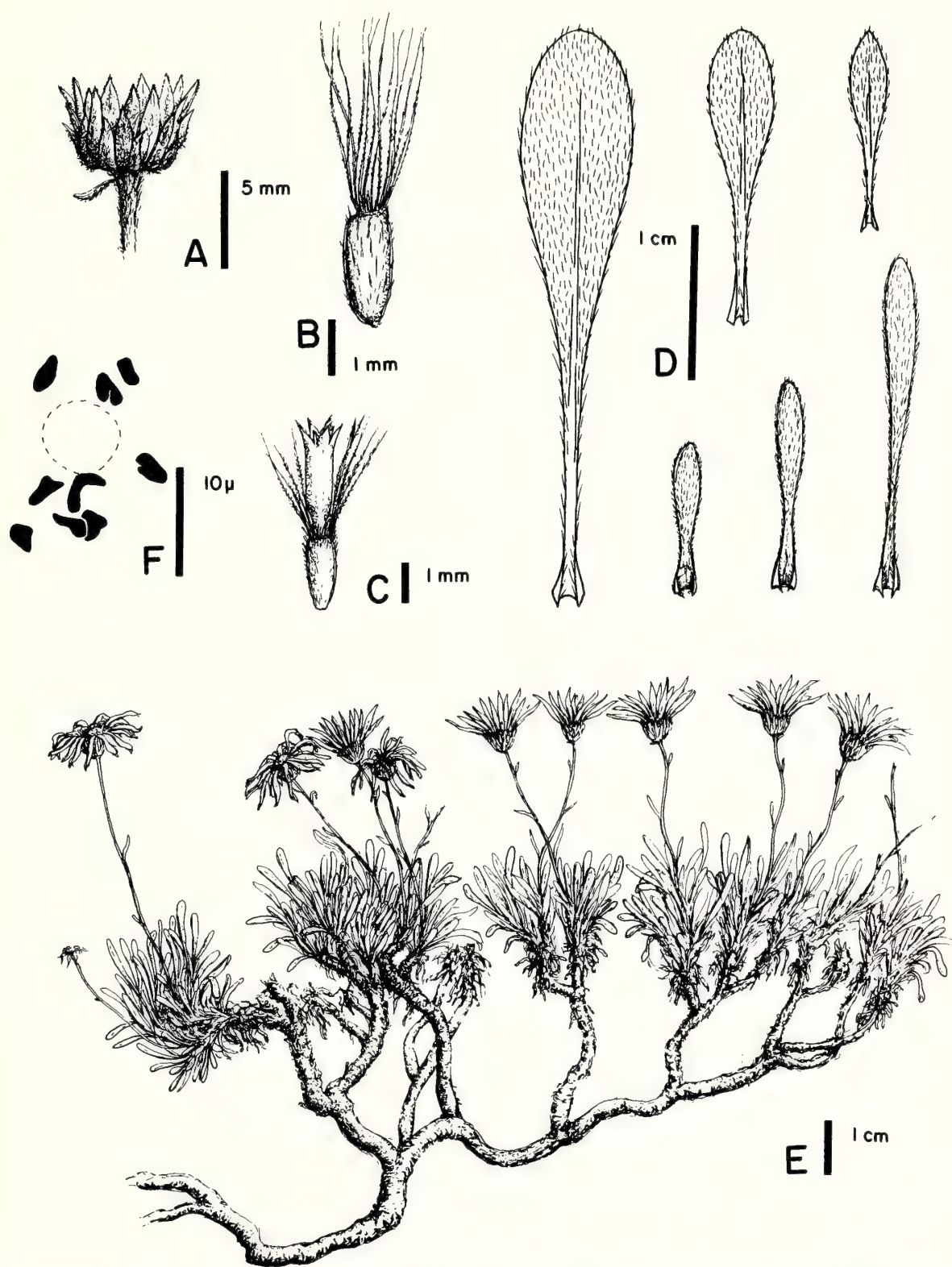


FIG. 2. *Erigeron acomanus* Spellenberg & Knight (drawn from the holotype, *Knight* 2689, unless otherwise indicated). (A) Involucre; (B) Cypsela (*Knight* 3613); (C) Disk flower; (D) Variation in leaves (upper set *Spellenberg* 4911, 4912, lower set from type); (E) Habit; (F) Late diakinesis in pollen parent cell,  $2n=9_{II}$ , (*Spellenberg and Ward* 9493).

dular-puberulent and lightly to moderately white-strigose. Ligules 16–30, white, 4.5–9 mm long, 1.3–1.8 mm wide. Disk corollas 2.5–3 mm long, yellowish, the triangular lobes often blushed with maroon. Cypselas somewhat flattened, ca. 2 mm long, 2-nerved, lightly



hirsute; pappus of 20–25 fine barbellate bristles 1.5–2.5 mm long, 0.8–1 times the length of the disk corolla; pappus bristles intermingled with a few shorter setae that are continuous with the hairs on the upper portion of the fruit. Chromosome number:  $n=9$ .

PARATYPES: USA, NM, McKinley Co., 5 mi N of US Highway 66 in Prewitt on road past power plant up Casomero Draw, 35°26'45"N, 108°02'40"W, elev. 7000 ft, 22 Jun 1985, *Barrie 1412* (COLO, NMC, TEX, US); ca. 2 mi N of Prewitt, T14N R21E sect. 24 NE ¼, elev. 6900 ft, 20 Jul 1983, *Fletcher 7074* (ALB); ca. 5 mi N of Prewitt, 7000–7100 ft, 30 Aug 1982, *Knight 1717* (TEX); 13 Aug 1986, *Knight 3416* (UNM); 3 Sep 1987, *Knight 3613* (UNM); Prewitt, behind Plains Electric power plant, 6 Jun 1985, *Spellenberg and Corral 8231* (NMC); ca. 2 mi N of Prewitt, T14N R12E sect. 24 NE ¼, 6800 ft, 31 May 1986, *Spellenberg 8497* (NMC); 31 May 1988, *Spellenberg and Ward 9493*, voucher for chromosome count  $2n=9_{II}$  (NMC); Valencia Co. (this area now in Cibola Co.), just E of Laguna Indian Reservation in Blue Water Canyon, ca. 13 air mi SE of Acoma Pueblo, T6N R7W boundary of sects. 25–36, 24 Sep 1977, *Spellenberg 4911, 4912* (NMC, NY).

*Distribution and habitat.* *Erigeron acomanus* is named for the Acoma Indian Pueblo. It was first discovered at the base of the cliffs that delimit the eastern boundaries of the lands of that tribe (*Spellenberg 4911, 4912*). At this site the species is restricted to shaded sandy slopes that build up beneath cliffs of Zuni Sandstone (Dane and Bachman 1957), which is derived from an eolian dune of upper Jurassic age (Maxwell 1975). At the type locality, near Prewitt, plants are also restricted to protected sandy slopes beneath cliffs of Entrada Sandstone of Jurassic age, which are capped by a gypseous limestone segment of the Todilto Formation (Smith 1954). Both sandstones degrade to produce a fairly coarse-grained alkaline sand.

At present, *E. acomanus* is known from only these two small populations and is being considered for federal protection by the U.S. Fish and Wildlife Service. There were perhaps 100 plants in the Blue Water Canyon population (*Spellenberg 4911, 4912*) in ca. ¼ hectare. At the type locality there are probably a few thousand plants along canyon bases in ca. 2 km<sup>2</sup>. However, the strata on which it occurs, and other related Mesozoic formations, extend intermittently along a 150-km east–west oriented crescent in west-central New Mexico (Green and Pierson 1977). Other populations of the species can be expected to occur in sheltered sandy places in this area. Where it is known to occur, common plant associates are *Pinus edulis* Engelm., *Juniperus monosperma* (Engelm.) Sarg., *Artemisia tridentata* Nutt., *Ribes cereum* Dougl., *Oryzopsis hymenoides* (Roemer & Schultes) Ricker, *Bouteloua gracilis* (Kunth) Lagasca, *Pentstemon barbatus* (Cav.) Roth, *Yucca angustissima* Engelm., *Gutierrezia sarothrae* (Pursh) Britt. & Rusby, *Aletes sessiliflorus* Theobald



& Tseng, and other species of either Intermountain or Madrean affinities.

*Morphology and relationships.* *Erigeron acomanus* is readily distinguished from other species of *Erigeron* in New Mexico by its monocephalic, leafy stems, round or obtuse leaf tips, white rays, and mat-forming habit. In Martin and Hutchins (1981) it keys with difficulty to near *E. vetensis* Rydb., but *E. vetensis* differs by its greater number of rays that are pink or blue and its herbage that is more or less densely glandular and at most sparsely hirsute (Cronquist 1947). In Cronquist, again with some difficulty, *E. acomanus* keys to *E. tener* of the Intermountain Region or to *E. cronquistii* Maguire, a very local species of northern Utah placed near to *E. tener* by Cronquist. Each unknown to the other, we sent our collections to Dr. Guy Nesom for identification. He suggested that we had disjunct material of *E. tener*.

*Erigeron acomanus* has white rays, has a mat-forming habit, and lacks peg-like glandular trichomes similar in shape to the "type C" trichomes illustrated by Nesom (1978) for another species. In contrast, labels on specimens of *E. tener*, when the color is given, consistently note the rays to be bluish or pinkish, descriptions consistent with those of Cronquist (1947) and Hitchcock et al. (1955). *Erigeron tener* also differs by its densely caespitose habit and by the presence of golden, peg-like, glandular trichomes on the stem. *Erigeron acomanus* also differs from *E. tener* by a number of quantitative features, most notably *E. acomanus* having generally shorter petioles, a greater number of leaves on the flowering stem, and a consistently monocephalic habit (Table 1). These differences, especially when considered with the disjunction in geographic ranges and differences in habitat, support the delimitation of *E. acomanus* as a species distinct from *E. tener*. Pappus bristles and habit readily distinguish *E. acomanus* from *E. cronquistii*. In the former there are 20–25 bristles that are about as long as the disk corolla; in the latter there are 12–20 bristles that are conspicuously shorter than the disk corolla (Cronquist 1947).

In little more than a decade two other narrowly endemic species of *Erigeron* have been described from New Mexico: *E. hessii* Nesom (1978) and *E. scopulinus* Nesom & Roth (1981), both more southern in distribution (Fig. 1). The relationship of *E. acomanus* may ultimately be shown to be with these. All are monocephalic and white-rayed, and perennate from a highly-branched subrhizomatous or rhizomatous caudex. *Erigeron acomanus* is more similar in habit and pubescence to *E. scopulinus* than to *E. hessii*. The three are, nevertheless, easily distinguished. *Erigeron hessii*, superficially similar to *E. acomanus* when pressed, is known only from about 3000 m in the Mogollon Mts. It has acute leaves, easily distinguished minute "type B" trichomes, and coarse "type A" trichomes (Nesom



TABLE 1. COMPARISON OF *ERIGERON ACOMANUS* WITH *E. TENER*. Values are for the mean  $\pm$  one standard deviation, with the range given in parentheses. p values for the differences between means are derived from Student's t-test. In making leaf measurements, the base of the blade was arbitrarily determined to be at the point where the width of the petiolar base becomes twice that of its narrowest point. *Erigeron acomanus* is represented from two sites; *E. tener* from 48 sites throughout the range of the species.

| Character   | <i>Erigeron acomanus</i><br>(n = 12) | <i>Erigeron tener</i><br>(n = 48) |
|---|--------------------------------------|-----------------------------------|
| Petiole length, mm<br>p = 0.0001                    | 7.4 $\pm$ 3.4 (3-13)                 | 19.8 $\pm$ 7.8 (7-40)             |
| Blade length, mm<br>p = 0.003                       | 11.0 $\pm$ 4.8 (8-23)                | 12.2 $\pm$ 3.5 (7-21)             |
| Blade width, mm<br>p = 0.05                         | 3.1 $\pm$ 1.3 (2-7)                  | 3.8 $\pm$ 1.0 (2-7)               |
| Plant height, cm<br>p = 0.10                        | 7.5 $\pm$ 2.9 (4.5-15)               | 8.8 $\pm$ 3.5 (2-19)              |
| Number of leaves on flowering<br>stem<br>p = 0.0001 | 6.5 $\pm$ 1.6 (4-10)                 | 3.6 $\pm$ 1.1 (2-6)               |
| Number of heads per inflorescence<br>p = 0.0001     | 1.0 $\pm$ 0.0 (1)                    | 1.7 $\pm$ 0.7 (1-4)               |
| Phyllary length, mm<br>p = 0.0001                   | 3.4 $\pm$ 0.4 (2.5-4.0)              | 4.0 $\pm$ 0.5 (3.0-5.1)           |
| Number rays per head<br>p = 0.004                   | 20.7 $\pm$ 4.8 (16-30)               | 25.0 $\pm$ 5.2 (16-40)            |
| Ray length, mm<br>p = 0.0003                        | 6.1 $\pm$ 1.3 (4.5-9.0)              | 4.7 $\pm$ 0.8 (3.3-7.0)           |

1978) 0.5-0.75 mm long with a density of 0-5/mm<sup>2</sup>. *Erigeron scopulinus* inhabits igneous cliffs. It is a mat-former with leaves rarely more than 12 mm long and flowering stems up to only 33 mm tall. "Type B" trichomes are not clearly present, but as in *E. acomanus* the "type A" trichomes are variable in size, the smallest resembling larger "type B" trichomes. Its "type A" trichomes are only about 0.17 mm long. On the adaxial leaf surface they have a density of about 20-35/mm<sup>2</sup>. In *Erigeron acomanus* the "type A" trichomes are 0.3-0.5 mm long and have a density of about 35-65/mm<sup>2</sup> (similar to length and density of trichomes in *E. tener*). Nesom and Roth (1981) discussed relationships of *E. scopulinus* with *E. cronquistii* and *E. tener* and noted that convergences and parallisms are prevalent among species of *Erigeron*. Critical studies of all these western forms are needed before relationships can be adequately evaluated.

ACKNOWLEDGMENTS

The early field work that resulted in the discovery of this taxon was supported by the Bureau of Land Management, Socorro District, New Mexico. We gratefully acknowledge the use of specimens and facilities at LL, NY, TEX, UC. We are also



indebted to Dr. Guy Nesom for help with our material, discussions with regard to the relationships of *E. acomanus*, and a review of a draft manuscript. To Rupert Barneby we express gratitude for an early reading of the manuscript. Thanks are extended to Darrell Ward for providing the chromosome count.

#### LITERATURE CITED

- CRONQUIST, A. 1947. Revision of the North American species of *Erigeron*, north of Mexico. *Brittonia* 6:121–300.
- DANE, C. H. and G. O. BACHMAN. 1957. Preliminary geologic map of the northwest part of New Mexico. U.S.G.S. map I-224.
- GREEN, M. W. and C. T. PIERSON. 1977. A summary of the stratigraphy and depositional environments of Jurassic and related rock in the San Juan Basin, Arizona, Colorado and New Mexico. Pp. 147–152 in N.M. Geol. Soc. Guidebook, 28th Field Conference, San Juan Basin III.
- HITCHCOCK, C. L., A. CRONQUIST, M. OWNBEY, and J. W. THOMPSON. 1955. Vascular plants of the Pacific Northwest, pt. 5, Compositae. Univ. Washington Press, Seattle.
- MARTIN, W. C. and C. R. HUTCHINS. 1981. A flora of New Mexico, Vol. 2. J. Cramer, Vaduz.
- MAXWELL, C. H. 1975. Geology map of the Acoma Pueblo Quadrangle, Valencia County, New Mexico. U.S.G.S. map GQ-1298.
- NESOM, G. L. 1978. *Erigeron hessii* sp. nov. and *Erigeron kuschei* Eastwood (Compositae), two closely related narrow endemics from the southwestern United States. *Brittonia* 30:440–446.
- and V. D. ROTH. 1981. *Erigeron scopulinus* (Compositae), and endemic from the southwestern United States. *J. Arizona–Nevada Acad. Sci.* 16:39–42.
- SMITH, C. T. 1954. Geology of the Thoreau Quadrangle, McKinley and Valencia counties, New Mexico. N.M. Bureau of Mines, Minerals Res. Bull. #31.

(Received 13 Jan 1987; resubmitted 3 Feb 1989; revision accepted 13 Mar 1989.)

## ANNOUNCEMENT

### TEMPORARY NEW ADDRESS FOR EDITOR OF MADROÑO

From 1 September 1989 to 18 December 1989 Dr. David J. Keil, Editor of MADROÑO, will be on sabbatical leave. Manuscripts, proofs, and other correspondence should be sent to:

DR. DAVID J. KEIL  
Department of Botany  
Arizona State University  
Tempe, Arizona 85287



## A RE-EVALUATION OF THE *ALLIUM SANBORNII* (ALLIACEAE) COMPLEX

STELLA S. DENISON and DALE W. MCNEAL  
Department of Biological Sciences,  
University of the Pacific,  
Stockton, CA 95211

### ABSTRACT

*Allium sanbornii* and related taxa present a confusing array from south-central Oregon to the Sierra Nevada foothills of central California. Previous attempts at classification have, generally, been unsuccessful due to a paucity of representative material. Herbarium and field studies were initiated to increase available material and to ascertain if previously overlooked characteristics could be found that would elucidate relationships within the group. Based on these investigations, *A. sanbornii* is divided into two varieties, var. *congdonii* and var. *sanbornii*, and two previously recognized varieties, var. *jepsonii* and var. *tuolumnense* are elevated to specific status. A key to, and distribution map of, the taxa are presented and relationships within the complex are discussed.

The *Allium sanbornii* complex belongs to a group of North American species referred to the *Allium sanbornii* alliance by Ownbey (Saghir et al. 1966). Species in the alliance are characterized by producing one single, terete leaf per bulb annually and having two prominent, flattened processes near the summit of each ovary lobe, forming a six-parted ovarian crest. As circumscribed by Ownbey (Munz 1959) the alliance consisted of eight species. This is the most distinctive of the nine North American alliances distinguished by Ownbey. However, it contains two species, *A. sanbornii* Alph. Wood, with four varieties, and *A. fimbriatum* S. Wats., with nine varieties that, as presently circumscribed, are extremely confusing. In the present paper we deal only with the taxa Ownbey attributed to *A. sanbornii*. *Allium fimbriatum* will be considered in a subsequent paper.

Members of the *Allium sanbornii* complex occur in the foothills of the Sierra Nevada in California from Butte Co. south to Mariposa Co. and at widely scattered locations from Tehama Co. north to central Jackson Co., Oregon. *Allium sanbornii*, originally described from along the Yuba River in Yuba Co., California, has been a much misunderstood species. Almost without exception, specimens bearing that name prior to investigation and annotation by Ownbey between 1946 and 1950 belonged to other species or at least not to the typical variety. Jepson's (1922) conception of *A. sanbornii* seems to have been drawn mainly from specimens of *A. jepsonii*, although



he did recognize and describe var. *congdonii*. Abrams' (1923) description, or at least his illustration, was drawn from specimens of var. *congdonii*. In southern California where none of these taxa occur, Munz (1935) used the name for the species now known as *A. howellii* Eastw. Ownbey (Munz 1959) recognized varieties, *jepsonii* and *tuolumnense*, which, though appearing in Munz, were never validly published by Ownbey. Their valid publication was finally accomplished by Traub (1972).

In Munz (1959) the latter two varieties are attributed to Ownbey and Aase, presumably because these two authors planned to publish a treatment of the *Allium sanbornii* alliance similar to their paper on the *Allium canadense* alliance (Ownbey and Aase 1955). No such paper was ever published and all of the specimens we have seen are annotated by Ownbey alone. For purposes of attribution therefore, we refer to these varieties along with several other taxa published by Traub (1972) as Ownbey ex Traub.

As has been pointed out previously, many investigators of *Allium* in western North America have been handicapped by a lack of representative material upon which to base taxonomic decisions. The *Allium sanbornii* complex represents an extreme example of this. At the time of Ownbey's annotation only 14 collections of var. *sanbornii* were available, several without locality data. Variety *congdonii* was represented by nine collections, var. *jepsonii* by five, and var. *tuolumnense* by a single collection.

*Allium* is a difficult genus and one in which pressing often obscures critical morphologic characters that are evident on fresh specimens. It is significant that Ownbey only observed two of the described varieties, *congdonii* and *jepsonii*, in fresh material. Because of this he did not observe critical features that might have suggested the alternative classification proposed here.

## METHODS

As part of a revision of *Allium* in California we have studied all of the available specimens from major American herbaria (CAS, CHSC, CPH, DAV, DS, GH, JEPS, MO, NY, POM, RSA, UC, US, WS) and have made extensive field observations. Voucher specimens and bulbs of putative taxa were collected over a 15-year period. Bulbs were grown at Stockton, California for determination of chromosome numbers for previously undetermined taxa. We used aceto-orcein squashes for all counts which were made on pollen mother cells from fresh buds.

## RESULTS

In the course of this investigation we made 19 new collections of the putative taxa of the *Allium sanbornii* complex. These gave us



ample opportunity to observe fresh material in the field and under cultivation for such characters as: condition and length of the leaf at anthesis, attitude of the perianth segments, and color of the flowers and anthers. The results of these observations are found in the taxonomic treatment which follows. The measurements given for each taxon in the taxonomic treatment represent both these new specimens and 55 specimens from the herbaria listed above or sent to the junior author for identification during his continuing investigations into the taxonomy of *Allium*.

In all taxa the chromosome number is  $n=7$ , the most common number for North American species.

Chromosome numbers for individual collections are given in the exsiccatae at the end of each species description (\* = unpublished count by Dr. Hannah C. Aase).

## TAXONOMIC TREATMENT

### KEY TO THE *ALLIUM SANBORNII* COMPLEX

- A. Stamens and style exserted; inner perianth segments 1.25–1.5 times longer than the outer. .... *A. sanbornii*
- B. Stigma  $\pm$  3-lobed, not distinctly trifid; perianth segments acute, anthers mostly yellow; anthesis late June–August. .... 1a. *A. sanbornii* var. *sanbornii*
- B' Stigma distinctly trifid; perianth segments acuminate to attenuate, anthers mostly purple; anthesis late May–June. ... 1b. *A. sanbornii* var. *congdonii*
- A' Stamens and style included; perianth segments  $\pm$  equal in length.
- C. Ovarian crest processes entire to  $\pm$  erose; perianth segments acute to apiculate, erect; known only from Butte Co. and Table Mt., Tuolumne Co., CA. .... 2. *A. jepsonii*
- C' Ovarian crest processes laciniate; perianth segments rounded, spreading; known only from Rawhide Hill and Red Hills, Tuolumne Co., CA. .... 3. *A. tuolumnense*

1. *ALLIUM SANBORNII* Alph. Wood, Proc. Acad. Nat. Sci. Philadelphia 20:171. 1868. See varietal headings for synonymy and typification.

Bulb ovoid, (8–)15–25 mm long, outer coat reddish-brown, chartaceous, cellular reticulation none or with 2–3 rows of vertical cells above the root pad, inner coats light brown or white. Scape 1.8–6.0 diam, terete. Leaf 1, terete above the tubular sheath, ca. equalling the scape, withering from the tip by anthesis. Bracts of the inflorescence 4, ovate, attenuate. Umbels compact, pedicels 18–190, narrow, 4–22 mm long. Perianth segments white to dark pink with darker mid-nerves, entire to erose, acute to acuminate or attenuate, outer segments 3–8 mm long, lanceolate to ovate, reflexed at the tips, inner segments 5–9 mm, ovate to broadly so, 1.25–1.5 times longer than the outer, stamens exserted, anthers ovate, mucronate, yellow or purple, style exserted, ca. as long as the stamens, stigma capitate,



obscurely 3-lobed or distinctly trifid; ovary crested with 6 conspicuous, triangular processes, the margins of which are entire to slightly irregular. Seeds black, finely reticulate, the cells granular.

- 1a. *ALLIUM SANBORNII* Alph. Wood var. *SANBORNII*.—TYPE: USA, California, Yuba Co., “prope Foster’s Bar (S. S. Sanborn) Aug.”, *Wood s.n.* (holotype, NY!; isotype consisting of a drawing from the holotype and a few flowers purportedly taken from the type, GH!).

Bulb (8–)15–20 mm long. Scape 1.8–5.4 dm. Pedicels 5–20 mm. Outer perianth segments lanceolate to ovate, inner segments ovate to broadly so, acute, the margins entire to more or less irregular, inner series 1.25 times longer than outer; anthers mostly yellow; stigma capitate to obscurely 3-lobed.

*Distribution.* Serpentine outcrops, 650–1350 m in the foothills at the north end of the Sacramento Valley, along the western slope of the Sierra Nevada from Shasta to Calaveras Co., California, and from a single, isolated population in central Jackson Co., Oregon (Fig. 1). Flowering late June–September.

Variety *sanbornii*, while not classified as threatened in any listing we have seen, consists of widely scattered, generally small populations that should be carefully monitored.

*Exsiccatae.* USA, CA, Butte Co.: Forbestown Rd 1.5 km E of Hurleton, 29 Jul 1980, *Ahart 2501* (CHSC); no locality, Jul 1878, *Bidwell s.n.* (GH); near Deer Creek, 24 Jul 1920, *Copeland 7* (DS); T25N R3E S13, 2.5 km N of jct. of Butte and Secret creeks, 29 Jul 1936, *Johannsen 970* (UC); Magalia, 20 Jul 1977, *Schlising 3197* (CHSC); T25N R3E S11, Hwy 32, 0.5 km S of Tehama City, 11 Sep 1980, *Schlising 3990* (CHSC); T21N R6E S27 NE of Oroville, 6 Aug 1983, *Schlising 4432* (CHSC); Paradise, 18 Jul 1940, *Wall s.n.* (CAS). Calaveras Co.: Ridge between Gardner and Big Tree Grove, 7 Aug 1906, *Dudley s.n.* (DS). El Dorado Co.: Sweetwater Creek, Aug, *M. Curran s.n.* (GH). Nevada Co., below McCourtney Rd, 5 km SW of Hwy 20 in Grass Valley, 18 Jul 1985, *Denison 53* (CPH) ( $n=7$ ). Shasta Co.: River Coram, 27 Jun 1914, *McMurphy s.n.* (DS, US). Tehama Co.: Deer Creek, Sep 1896, *Austin s.n.* (US); Deer Creek Meadows, Sep 1896, *Bruce 549* (MO). County and locality unknown: *Pratten s.n.* (NY); *Shelton s.n.* (NY); *Shevrns s.n.* (MO); *Wallace s.n.* (GH). OR, Jackson Co.: T36S R10W S25, SE of town of Gold Hill, Aug 1988, *Callahan s.n.* (CPH).

- 1b. *ALLIUM SANBORNII* Alph. Wood var. *CONGDONII* Jepson, Fl. Calif. 1:275. 1922.—TYPE: USA, California, Mariposa Co., Benton Mills Rd, 3 Jun and 12 Jul (according to the label), *Congdon s.n.* (holotype, UC!; specimen with almost illegible label presumed to be an isotype, POM!).



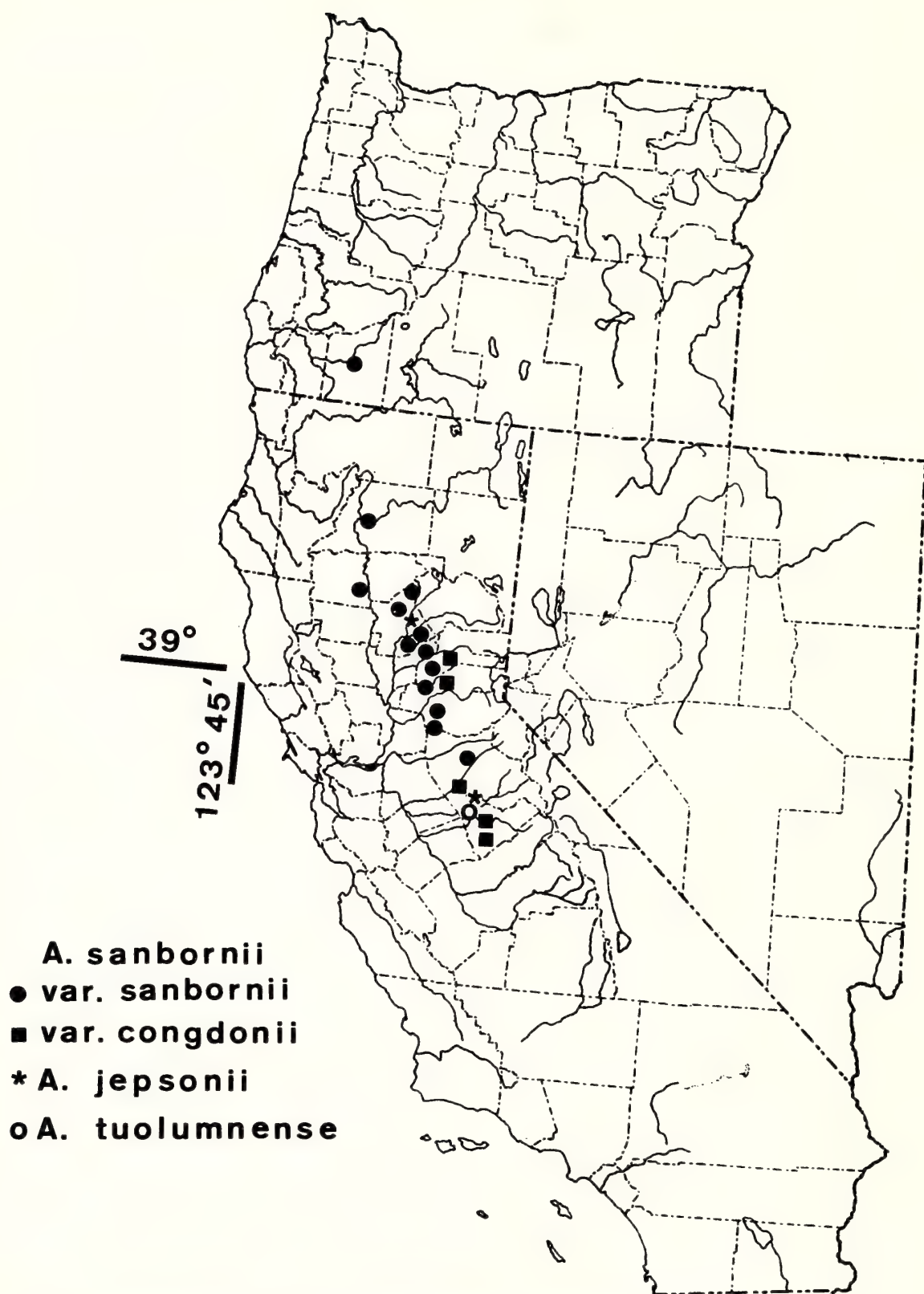


FIG. 1. Distribution of the *Allium sanbornii* complex.

*Allium intactum* Jepson, Fl. Calif. 1:273. 1922.—TYPE: USA, California, Placer Co., Cape Horn, 18 Jul 1908, *M. Brandege* s.n. (holotype, JEPS!).

Bulb 15–25(–30) mm long. Scape 2.4–6.0 dm. Pedicels 5–22 mm. Perianth segments ovate to broadly so, acuminate to attenuate,



margins more or less erose, inner series 1.5 times longer than outer; stigma distinctly trifid.

*Distribution.* Disjunct on serpentine outcrops between 350 and 650 m in Nevada, Placer, Tuolumne, and Mariposa cos., California (Fig. 1). Flowering late May to mid-July.

Plants of variety *congdonii* are taller and more robust than those of var. *sanbornii*. The varieties are clearly distinct on the characteristics noted above and in the key; there is no difficulty in distinguishing them. Variety *congdonii* is the most commonly encountered member of the *A. sanbornii* complex and frequently occurs in large populations.

*Exsiccatae.* USA, CA, Mariposa Co.: Josephine Mine, 3 Jun 1893 (1899?), *Congdon s.n.* (POM); 5 km NW of Coulterville, 15 Jun 1937, *Hoover 2470* (WS, UC); T4S R17E sect. 8, Hwy 49, 3 km N of Bear Valley, 8 Jun 1972, *McNeal 1056* (ASC, ASU, BRY, CPH, NY); 0.5 km N of summit, Bear Valley–Bagbey Rd, 29 Jun 1933, *Wolf 5114* (WS, RSA). Nevada Co.: S fork of Yuba River, ca. 1 km W of Washington, 5 Jul 1984, *Denison 49* (CPH); 3.5 km N of Hwy 20 on rd to Washington, 5 Jul 1984, *Denison 50* (CPH) ( $n=7$ ); 4 km N of Hwy 20 on rd to Washington, 14 Jul 1963, *Mann and Mann s.n.* (DAV); S fork of Yuba River ca. 1 km W of Washington, 24 Jun 1976, *McNeal 1952* (CPH). Placer Co.: S bank of American River, 1.5 km NE of bridge on Colfax–Iowa Hill Rd, 22 Jun 1952, *Stebbins 5100* (CAS, DAV). Tuolumne Co.: Hwy 49, 100 m N of the Mariposa Co. line, 19 Jun 1984, *Denison 48* (CPH); 9 km N of Coulterville, 4 Oct 1948, *Hoffman 2400* (WS); Hwy 49, 100 m N of the Mariposa Co. line, 10 Jul 1971, *McNeal 603* (CPH, WS); T1N R14E S8, above Rawhide Rd, 6 Jun 1972, *McNeal 1011* (BRY, CPH); T2S R16E S7 above Hwy 49, 3 km N of the Mariposa Co. line, 8 Jun 1972, *McNeal 1034* (CPH, IDS, NY, OSC); T1N R14E S5, just E of French Flat, 30 Jun 1946, *Ownbey and Ownbey 2965* (WS); T1N R14E S5, 1 km ESE of French Flat, 9 Jun 1935, *Rutter 238* (UC).

2. *Allium jepsonii* (Ownbey ex Traub) Denison & McNeal, stat. et comb. nov.—*Allium sanbornii* Alph. Wood var. *jepsonii* Ownbey ex Traub, Pl. Life 28:63. 1972.—TYPE: USA, California, Tuolumne Co., Table Mt. above Rawhide Hill 600 m, 23 May 1919, *Mrs. W. J. Williamson 157* (holotype, DS!; isotypes, CAS!, POM!, US!, WS!). In the protologue, Traub (1972) cites additional specimens (CPH!, UC!, WS!) dated 30 May, with the same locality data and collection number. We consider these to be paratypes. One of the specimens at WS lacks a collection date. After comparing the specimens and the labels on the ho-



lotype, isotypes, and paratypes we conclude that the collection date should be 23 April and that this specimen is an isotype.

Bulb ovoid, (11–)15–25 mm long, outer coat grey-brown, chartaceous, cellular reticulation none or with 2–3 rows of vertical cells above the root pad, inner coats light brown to white. Scape 25–37 cm. Leaf ca. equalling the scape, withering from the tip by anthesis. Spathe bracts 3–4, ovate, attenuate. Umbel loose, 20–60+ flowered, pedicels 7–20(–25) mm. Perianth segments white, flushed with pink near the dark pink mid nerve, outer series 7–8.5 mm, the inner 6–8.5 mm, ovate-elliptic, acute to apiculate, margins erose, outer series erect with reflexed tips, the inner erect; stamens well included, anthers mostly yellow, style included, stigma distinctly trifid; crest processes with erose margins. Seeds black, finely reticulate, the cells granular.

*Distribution.* Serpentine soils in the Sierra Nevada foothills, Butte Co.; volcanic soil on Table Mt., near Jamestown, Tuolumne Co., California (Fig. 1). Flowering late May to June.

*Allium jepsonii* is clearly related to *A. sanbornii* but differs in its grey-brown, chartaceous bulb coats, loose umbels and  $\pm$  equal perianth segments. We are presently at a loss to explain the disjunct distribution of this species, but note that similar or larger disjunctions occur along the west base of the Sierra Nevada in *A. cratericola* Eastw. and *A. peninsulare* Lemmon ex Greene. *Allium jepsonii* can be looked upon as consisting of only two populations, with the Tuolumne Co. one being quite small, it is rarely encountered or collected and while currently not considered threatened it should be considered for listing and carefully monitored.

*Exsiccatae.* USA, CA, Butte Co.: Jarboe Pass, 5 Jun 1940, *Heller 15703* (DS, MO, US); Ponderosa Rd at W fork of Feather River, 8 Jun 1952, *Hoffman 4082* (WS) ( $n=7^*$ ); T22N R4E S17 ca. 100 m E of Jordon Hill Rd, 22 Jun 1978, *Jokerst 151* (CHSC); W branch of Feather River, 28 Feb 1952, *Staley s.n.* (CHSC); T22N R4E S23 W side, Ponderosa Way, 0.7 km N of Jarbo Gap, 24 Jun 1982, *Taylor 4750* (CHSC). Tuolumne Co.: Table Mt., above Rawhide, 8 Jun 1984, *Denison 47* (CPH); top of Table Mt. opposite Rawhide Hill, 29 May 1980, *McNeal 2329* (CPH, NY).

***Allium tuolumnense*** (Ownbey ex Traub) Denison & McNeal, stat. et comb. nov.—*Allium sanbornii* Alph. Wood var. *tuolumnense* Ownbey ex Traub, Pl. Life 28:63. 1972.—TYPE: USA, California, Tuolumne Co., Canyon of Spring Gulch on Rawhide Hill, 375 m, 12 May 1919, *Mrs. W. J. Williamson 64* (holotype, DS!; isotypes, CPH!, UC!, US!, WS!).

Bulb ovoid, (10–)13–20(–25) mm long, outer coat dark reddish brown, brittle, cellular reticulation none or with 2–3 rows of vertical



cells above the root pad, the inner light brown, ligneous. Leaf ca. equalling the scape, withering from the tip by anthesis. Bracts usually 3, ovate, attenuate. Umbel loose, 20–60+ flowered; pedicels 7–20 (–23) mm. Perianth segments white or flushed with pink, 6–8 mm, spreading from the base, entire, broadly ovate to nearly round; stamens well included, anthers yellow; stigma included, distinctly trifid; ovarian crest processes laciniate. Seeds black, finely reticulate, the cells granular.

*Distribution.* Serpentine soil, Sierra Nevada foothills of Tuolumne Co., California, 400–600 m, known only from populations on Rawhide Hill near Jamestown and in the Red Hills south and west of Chinese Camp (Fig. 1). Flowering late March to early May.

*Allium tuolumnense* is a highly restricted endemic differing from *A. sanbornii* and *A. jepsonii* in its entire, spreading perianth segments, laciniate ovarian crest processes, and March to early May blooming period which does not overlap with either of the other species. In these characteristics, *A. tuolumnense* resembles *A. howellii* of the South Coast Ranges from which it differs in its extremely broad, almost round perianth segments, and included stamens.

*Allium tuolumnense* is currently listed as rare and endangered by the California Native Plant Society (Smith and Berg 1988) and in candidate status Category 1 by the U.S. Fish and Wildlife Service (1983). It occurs in only three scattered populations and is endangered by recreational use and proposed development of significant portions of its habitat.

*Exsiccatae.* USA, CA, Tuolumne Co.: T1N R14E sect. 8, Rawhide Hill, 30 Apr 1984, *Denison 44* (CPH) ( $n=7$ ); Rawhide Hill, 20 Apr 1985, *Denison 51* (CPH); Rawhide Hill, 20 Apr 1985, *Denison 52* (CPH); Rawhide Hill, 6 Apr 1972, *McNeal 718* (CPH, NY, WS); Rawhide Hill, 22 Apr 1972, *McNeal 781* (BRY, CPH); Rawhide Hill, 27 Apr 1973, *McNeal 1295* (ASU, CPH); T1S R14E S5, Red Hills, above Sims Rd, 1 km S of Hwy 120, 3 May 1973, *McNeal 1304* (CPH, NY, OSC); T1S R14E S17, Red Hills, above Redhills Rd 3 km S of Hwy 120, 12 May 1975, *McNeal 1601* (CPH, NY); T1S R15E S27, Hwy 120, 1 km NW of Moccasin, 6 Apr 1988, *Stone 872* (CPH); T1S R14E S17, Redhills SE of Chinese Camp, 22 Apr 1985, *Taylor 8606* (CPH); T1S R14E S17, Red Hills on rd to landing strip, 11 May 1980, *Willoughby 4455* (CPH); Rawhide Hill ca. 1 km E of Rawhide Flat, 11 May 1980, *Willoughby 4464* (CPH); Rawhide Hill ca. 1 km E of Rawhide Flat, 11 May 1980, *Willoughby 4465* (CPH).

#### ACKNOWLEDGMENTS

Critical reviews by M. Beauchamp, T. D. Jacobson, and F. H. Utech were very helpful in preparing this paper. We gratefully acknowledge the Faculty Research



Committee and the F. R. Hunter Memorial Fund of the University of the Pacific for their support of the investigation.

#### LITERATURE CITED

- ABRAMS, L. R. 1923. An illustrated flora of the Pacific states, Vol. 1. Stanford Univ. Press, Palo Alto, CA. 557 pp.
- JEPSON, W. L. 1922. A flora of California. 1(6):270–280. Student Book Store, Univ. of California, Berkeley.
- MUNZ, P. A. 1935. Manual of southern California botany. Claremont Colleges, Claremont, CA. 642 pp.
- . 1959. A California Flora. Univ. California Press, Berkeley, CA. 1681 pp.
- OWNBEY, F. M. and H. C. AASE. 1955. Cytotaxonomic studies in *Allium* I. *Allium canadense* alliance. Res. Stud. State Coll. Wash. 23(Suppl.):1–106
- SAGHIR, A. R. B., L. K. MANN, M. OWNBEY, and R. Y. BERG. 1966. Composition of volatiles in relation to taxonomy of American *Alliums*. Amer. J. Bot. 53:477–484.
- SMITH, J. P., Jr. and K. BERG (eds.). 1988. Inventory of rare and endangered vascular plants of California. Special Publication No. 1, 4th ed. California Native Plant Society, Sacramento, CA. 168 pp.
- TRAUB, H. P. 1972. *Allium* species and varieties. Pl. Life 28:63–64.
- U.S. FISH AND WILDLIFE SERVICE. 1983. The U.S. list of endangered and threatened wildlife and plants. Federal Register 48(145):34182–34196.

(Received 24 Oct 1988; revision accepted 27 Feb 1989.)



## NOTES

*MYOSOTIS LATIFOLIA* AND NOT *M. SYLVATICA* (BORAGINACEAE) IN CALIFORNIA.—Considerable confusion has existed around the names *M. latifolia* Poir. and *M. sylvatica* Hoffm. in California. Jepson (Manual Flowering Plants California, 1925, 1943), Abrams (Illustr. Fl. Pacific States, 1959), and Munz (A California Fl., 1959) referred to all California material as *M. sylvatica*. Several recent local floras (Howell and Howitt, Monterey Fl., Wassman J. Biol. 22, 1964; Howell, Marin County Fl., 1970; and Thomas, Flora Santa Cruz Mts., California, 1961) use "*M. latifolia* (= *M. sylvatica*)." Howell states in his supplement that *M. latifolia* is the correct name for what had previously been called *M. sylvatica*. Munz, in his Supplement to A California Fl. (1968), cites Johnston (Wrightia 2:16–17, 1959) in using *M. latifolia* to replace the name *M. sylvatica*.

It seemed that these authors were saying that the two names represent a single taxon. Index Kewensis (1895) originally gave *M. latifolia* as a synonym of *M. sylvatica* though this later proved to be incorrect (*M. sylvatica* was published in 1791; *M. latifolia* in 1816). Grau (Osterr. Bot. Zeitschr. 111:561–617, 1964) and Grau and Merxmüller (Flora Europaea, 3:111–117, 1972) recognize the two taxa as distinct.

Grau's 1964 monograph of the genus cites one collection of *M. latifolia* from North America: Kalifornien, Mill Valley (Marin Co.); Meebold III, 1930 (M). The California material that I have seen while preparing the treatment for the revised Jepson Manual (ca. 100 sheets from CAS, DS, JEPS, NY, RSA, and UC) date from the turn of this century to the present. The collections are labelled *M. sylvatica*, *M. latifolia*, or are annotated with both names. These are all *M. latifolia* to which the name *M. sylvatica* was long ago misapplied. *Myosotis latifolia* has expanded its native range from the Azores and Canary Islands to areas with a climate similar to its original Mediterranean one; *M. sylvatica*, a Eurasian native, can be found infrequently in eastern North America but has not been collected on the Pacific Coast.—ELAINE JOYAL, Desert Botanical Garden, 1201 N Galvin Parkway, Phoenix, AZ 85008. (Received 6 Jan 1989; revision accepted 13 Mar 1989.)

MOONWORTS (*BOTRYCHUM*: OPHIOGLOSSACEAE) IN THE JONESVILLE AREA, BUTTE AND TEHAMA COUNTIES, CALIFORNIA.—The area in and around Jonesville has proved to be the most productive for botrychiums yet reported in California. Of the six species now known in the area, three involve range extensions, two of them new to the state flora.

The moonworts comprise *Botrychium*, subg. *Botrychium* (Ophioglossaceae). The type is the widespread and often common moonwort, *B. lunaria* (L.) Sw. of cold-temperate regions of the northern and southern hemispheres. Oddly, *B. lunaria* has evidently not been found in California. Munz's reports (A California Fl., 1959, p. 30) of *B. lunaria* and *B. lunaria* var. *minganense* are based on forms of the similar *B. crenulatum* (see below). Most moonworts require intensive searching before any specimens are found, and more often than not, no specimens are found. Most are very rare, and they are difficult to see because of their small size and their tendency to be overtopped by forbs and graminoids. They are sensitive to drought and may not appear in very dry, hot years. Compared to those of New England or of the Great Lakes region, the moonworts of California are poorly known; only four species have previously been recognized, two of which range as far south at high altitudes as the San Bernardino Mountains. In this paper we report new records from the Jonesville area in Butte and Tehama counties, which is the richest area for these plants thus far discovered in the state.



Jonesville is located in the southern Cascade Mountains, approximately 35 miles (55 km) NE of Chico. The earliest collections of *Botrychium* in Jonesville were those by E. B. Copeland, who distributed numerous specimens of *B. simplex* taken in 1931 in a meadow near his home. In July 1949, Wagner found many individuals of two species, *B. crenulatum* and *B. simplex*, in a meadow near Jonesville. In July 1985 and August 1986, Devine made intensive leaf collections mainly along Willow Creek that are notable not so much for their numbers as for their diversity.

The habitats studied by Wagner were in a damp, springy meadow, about 1 mile NNW of Jonesville, ca. 270 m W of Willow Creek, just below a dirt road parallel to it. The botrychiums grew along the upper edge of the meadow, usually on tussocks and rises around isolated trees where the ground was not so wet. The most conspicuous associated genera were *Hypericum*, *Liparis*, *Mimulus*, and *Veratrum*. *Botrychium crenulatum* was locally abundant here, *B. simplex* only frequent. The large evergreen grapefern, *Botrychium multifidum*, (subg. *Sceptridium*) was represented by a few plants along the dry edge of the meadow.

The habitats investigated by Devine were mainly along a 3.6-km stretch of Willow Creek, running from 1500 to 1800 m in Butte and Tehama counties. Some additional specimens were taken beside Jones Creek at its junction with Humboldt Rd. The plants were in mixed conifer forest on creek banks, clearings, and in the forest growing on more or less damp soil under sedges or on organic soil, often with mosses built up at the bases of the conifers. In approximate order of their association with the botrychiums, the conifers were *Abies concolor*, *Calocedrus decurrens*, *Pinus lambertiana*, and *P. ponderosa*. The most common herbaceous associates were *Carex* spp., *Circaea alpina*, *Listera convallarioides*, *Mimulus floribunda*, and *Viola macloskeyi*. Less common were species of grasses, *Hypericum*, *Lilium*, *Perideridia*, and *Sisyrinchium*. Among the least common associated genera were *Aquilegia*, *Equisetum*, *Pteridium*, *Stellaria*, and *Veratrum*. Out of the total of 67 leaf specimens, each representing a separate plant gathered by Devine, *Botrychium minganense* was the most common with 34 in all. *Botrychium montanum* numbered 16, *B. crenulatum* 9, *B. ascendens* 7, and *B. simplex* only 2. Vouchers will be deposited at MICH and UC.

#### KEY TO *BOTRYCHIUM* SPECIES AT JONESVILLE

The key below includes *B. multifidum* (Gmel.) Rupr. belonging to subg. *Sceptridium*; all the other taxa are typical moonworts.

- a. Sterile portion of leaf mostly well over 10 cm long, 3- to 4-divided, evergreen; leaf primordium (inside basal sheath) hairy. . . . . *B. multifidum*
- a' Sterile portion of leaf mostly less than 10 cm long; 1-divided or merely lobed, deciduous; leaf primordium glabrous.
  - b. Sterile portion 1-pinnate, the pinnae spatulate, cuneate, or flabellate.
    - c. Pinnae flabellate, the lower ones with upper and lower borders at angles of mostly 100° or more; margins subentire to crenulate-dentate. . . . . *B. crenulatum*
    - c' Pinnae cuneate to subflabellate, the lower ones with upper and lower borders at angles of 40–100°; margins entire or subentire, or finely and irregularly lacerate.
      - d. Pinnae distally rounded, entire; not or only slightly ascending; lower pinnae widely cuneate to subflabellate, forming angles of 50–100° (sometimes more); basal pinnae lacking supernumerary sporangia. . . . . *B. minganense*
      - d' Pinnae distally angular, the outer margin lacerate; ascending; lower pinnae cuneate, usually less than 50°; basal pinnae commonly with supernumerary sporangia. . . . . *B. ascendens*
  - b' Sterile portion merely lobed at base to simple (sometimes with one or two pinna pairs in *B. simplex*).
    - e. Lobes and tip rounded, the outer margins smooth; texture herbaceous; plants of wet lawns and open meadow areas. . . . . *B. simplex*





FIG. 1. Silhouettes of *Botrychium* leaves from Jonesville, California. Except as noted, all specimens taken by Devine in 1985–1986. A. *B. crenulatum* (3 on right, *Wagner* in 1947, UC). B. *B. ascendens*. C. *B. minganense*. D. *B. montanum*. E. *B. simplex* (5 on left, *Wagner* in 1947; 2 on right, *Copeland* in 1931 (MO, CA).

e' Lobes and tip irregularly angular, the outer margins more or less coarsely dentate; texture succulent; plants of shaded coniferous forest floors. ....  
..... *B. montanum*

Following are some notes on the species:  
*Botrychium crenulatum* W. *Wagner* (Fig. 1A). This species was originally described from the San Gabriel Mountains of southern California. Since its original publication (1981), we have learned that this moonwort has an extensive range, and is more



variable than we first thought. It is now known to range as far north as Oregon, Montana, and Alberta, and as far east as Utah, but is very rare and local. It grows mainly in wet meadows (Wagner 4609, UC), often with *B. simplex*. Along Willow and Jones Creek, Devine found only a few specimens (Devine 0840b, 0842b, 0895). It may be distinguished from *B. lunaria*, which is its nearest relative, on the basis of numerous characters (Amer. Fern J. 71:20–29) especially the small size, yellowish (not bluish) color, and the crenate (not entire) margins.

*Botrychium minganense* Victorin (Fig. 1C). This is the most frequent moonwort along Willow Creek (Devine 0839, 0840, 0841b, 0842a, 0844a, 0847, 0851, 0880.2, 0894, 0896). The Mingan moonwort is one of the most widespread North American species, occurring in practically all parts of Canada and Alaska, and ranging widely in the western United States mountains, south to Arizona. For many years this species was confused with *B. lunaria*, and even after the careful studies of Victorin, authors continued to treat it as a variety or form of that species. A detailed comparison of the two taxa is given by Wagner and Lord (Bull. Torrey Bot. Club 83:261–280, 1956).

*Botrychium ascendens* W. Wagner (Fig. 1B). This extremely rare western species is known from the Yukon Territory south to Oregon, Nevada, and California. It most closely resembles *B. crenulatum* but differs in the narrowly cuneate and strongly ascending segments (rather than flabellate and not or only slightly ascending segments), sharply serrate or lacinate outer pinna margin (rather than crenulate to denticulate), and the tendency for supernumerary sporangia to develop on the basal pinnae. The new collections are Devine 0841b, 0844b, 0848, 0853, and 0893. Also, *B. ascendens* differs in being a tetraploid ( $n=90$ ) unlike *B. crenulatum* which is a diploid ( $n=45$ ) as reported by Wagner and Wagner (Amer. Fern J. 76:33–47, 1986). *Botrychium ascendens* was first reported from California on the basis of information from Wagner by Lellinger (A field manual of ferns and fern allies, Smithsonian Inst., Washington, D.C., 1984). The single plant upon which the record is based was taken at Camp Agassiz in the Lake Tahoe Region (Alice Eastwood in 1906, CAS), approximately 140 km ESE of Jonesville.

*Botrychium simplex* E. Hitchc. (Fig. 1E) is by far the most frequent and variable moonwort species in California. It has an enormous range in North America extending from high elevations in southern California and North Carolina northward to Alaska and Newfoundland, and is also widespread in the Old World. Although it is generally regarded as rare, it is probably much more common than usually assumed. The sterile portion of the frond varies from simple to pinnate, and the attachment varies from ground level to high on the common stalk. In California its habitat is apparently always in open, grassy areas, often more or less marshy. In some localities (e.g., San Bernardino Mts., Yosemite Natl. Park) the sterile blade at maturity becomes broadly ternate with three main branches, each of them pinnate. This form has not been seen in the Jonesville area. Copeland first discovered *B. simplex* on his property at Jonesville, growing “in damp meadows, with sedges (notably *Carex aurea*), grasses, *Mimulus primuloides*” (Meadow below house, 1500 m, 11 Jun 1931, Copeland 601, UC, NY, UCLA, US). Wagner found it growing with, but much less common than, *B. crenulatum* on 16 Jul 1949 (Wagner 4710, UC). Devine found only two individuals along Willow Creek in 1985–1986 (Devine 0845b, 0846b).

*Botrychium montanum* W. Wagner (Fig. 1D). At the time of its description (Wagner and Wagner, Amer. Fern J. 71:20–30, 1981), we knew this rare moonwort only from Montana. Now we have records from western British Columbia, Washington, and Oregon (Wagner unpubl.). In general, it prefers rich, shaded coniferous forest, where it sometimes forms large local colonies. The new finds of *B. montanum* (Devine 0839a, 0845a, 0846c, 0880.1, 0892, 0895.2) represent a major range extension for the species and the first records for California. The plants may be distinguished from other Jonesville moonworts by their long-petioled sterile blades, the latter irregularly lobed and the outer margins toothed or lacerate. Unlike those of any of the numerous forms of *B. simplex*, the segments are angular, not rounded, and the apex is irregularly dissected, not entire.



From the results so far, with six taxa already found, the Jonesville area promises to be an excellent place to continue exploration for moonworts and other grapeferns. Other species that should be sought here include *B. lunaria*, *B. lanceolatum* (Gmel.) Angstr., *B. pinnatum* St. John, and *B. virginianum* (L.) Sw. The new records are all species previously known from Oregon. They are the sole records for California and should at present be regarded as threatened species. It is to be hoped that collectors will not remove whole plants under any circumstances. If leaves only are taken, the stem and roots being left in place, the plants will remain alive and continue to grow.

We are grateful to Alan R. Smith, pteridologist of the University of California, for his overall help in this investigation, to Florence S. Wagner for field assistance, and G. A. Yatskievych for aid on the manuscript. — WARREN H. WAGNER, JR., Department of Biology, The University of Michigan, Ann Arbor, MI 48109, and TIMOTHY B. DEVINE, Department of Biological Sciences, California State University, Chico, CA 95929-0516. (Received 24 Oct 1988; revision accepted 27 Feb 1989.)

Note added in proof: We thank Kenneth A. Wilson for the following additional California record of *B. manganense* (the specimen originally identified as *B. simplex*) approximately 400 km SSE of Jonesville: Fresno Co., King's River, 2nd fork below Palisade Creek, A. J. Perkins Herb., 24 Jul 1920 (LAM).

*SALIX SCOULERIANA* J. BARRATT EX HOOK. (SALICACEAE) IN SONORA, MEXICO. — In a recent paper on *Salix scouleriana* in Mexico (Argus, Madroño 35:350–352, 1988) I reported the occurrence of this boreal species in Coahuila, Mexico. At that time I was unaware that it occurred elsewhere in Mexico.

While working on California *Salix* in the United States National Herbarium I came across a specimen of this species collected by Edgar A. Mearns in 1893 in Sonora, Mexico. It was identified as *S. nuttallii* Sargent (a common synonym of *S. scouleriana*). Because the label lacked the name of a country or state it was misfiled with California specimens. The specimen label data are: E. A. Mearns 1783, Johnston's Ranch near Monument No. 88 (San José Mt.), 12 Aug 1893 (US 232468).

In his report, *Mammals of the Mexican Boundary of the United States* (U.S. Natl. Mus. Bull. 56, 1907), Mearns presents an annotated list of the trees of the "Mexican Boundary line" and gives detailed descriptions of the vegetation at his collecting localities. San José Mountain is located 8.5 km (5.25 mi) south of the Arizona border and 386 km (240 mi) west of the Río Grande (measured along the International Boundary). Its approximate latitude and longitude are 31°15'N and 109°58'W. The mountain begins at a base level of 1308 m (4265 ft) and rises abruptly to 2541 m (8337 ft). "Timber line begins near the base of the cone on the north side, but considerably higher on the south. This mountain is wooded with aspen and deciduous white oak at the summit. . . ." *Salix scouleriana* was collected between a small spring on the north side at 1830 m (6000 ft) and the main summit. — GEORGE W. ARGUS, National Herbarium of Canada, Museum of Natural Sciences, Box 3443, Sta. D., Ottawa, K1P 6P4, Canada. (Received and accepted 4 Feb 1989.)

TYPEFICTION OF *SALIX GEYERIANA* (SALICACEAE). — *Salix geyeriana* was described by N. J. Andersson in 1858 (Proc. Amer. Acad. Arts 4:63, also in Öfvers. Förh. Kongl. Svenska Vetensk.-Akad. 15:125, 1858). The only collection cited was Geyer 286. Geyer (London J. Bot. 5:289, 1846) indicated that he collected this number on the Coeur d'Alaine River, presently in Idaho. Andersson sometimes indicated where he saw a collection when describing a new species, but he did not for the Geyer collection. Geyer's duplicate sets were placed on sale through the Royal Botanic Gardens, Kew (London J. Bot. 4:482, 1845) so the primary set was likely at K. Geyer 286 is not at S (Kåre Bremer pers. comm.), the location of many of Andersson's types. In the 1858 papers, Andersson indicated seeing other collections of willows in "Herb. Hook." so this is likely where he saw Geyer 286.



Having seen a fragment of this collection earlier at A, I thought (Rhodora 79:415, 1977) that it could represent what is presently called *Salix lemmonii* Bebb. I have now been able to examine the Geyer collection from the Hooker Herbarium at K. The sheet contains two specimens, one pistillate and one staminate. Both are rather immature but still display enough characteristics for determination. The staminate specimen has densely hairy year-old branchlets which are not pruinose, elongate flower bracts which are tan and bear long hairs, and broadish leaves with no reddish hairs. In comparison with a series of specimens from northern Idaho, this can be identified as *S. bebbiana* Sarg. The pistillate specimen has glabrate and pruinose year-old branchlets, elongate flower bracts which are tan and bear short hairs, short aments, slender and elongate capsules which are densely hairy, stipes about as long as the bracts, and narrow leaves with some reddish hairs on the younger ones. This specimen easily falls within the variation of what is presently called *S. geyeriana*. The pistillate specimen is therefore designated the lectotype. Andersson's primary description appears to be drawn from this specimen. His comparison to *S. vagans* includes both pistillate and staminate characteristics.

I thank Kåre Bremer for checking for the Geyer collection at S. The loan of the Geyer collection from K and the use of facilities at RM are acknowledged. Finally, I thank George Argus and Paul Silva for their comments on the original manuscript. — ROBERT D. DORN, Box 1471, Cheyenne, WY 82003. (Received 11 Dec 1987; revision accepted 18 Jan 1989.)

---

## NOTEWORTHY COLLECTIONS

### ARIZONA

*EPHEDRA FUNEREA* COV. & MORTON (EPHEDRACEAE).—La Paz Co., ca. 13 km N of Bouse on Swansea road to Midway, near bench mark 1230, T8N R16W S21, between stabilized sandhills with *Larrea divaricata* ssp. *tridentata*, *Ambrosia dumosa*, and *Opuntia ramosissima*, 408 m, 3 Mar 1980, *Butterwick 5675 and Hillyard* (ASU); La Paz Co., 6.4 km N of Bouse, T8N, R17W, S26, May 1981, *Norris 1354, 1355* (ASU).

*Previous knowledge.* Known from S CA and S NV. This species is listed as *Ephedra californica* S. Wats. var. *funerea* (Cov. & Morton) L. Benson by Benson and Darrow (Trees and shrubs of the southwestern deserts, 3rd ed., University of Arizona Press, Tucson, AZ, 1981).

*Significance.* First records of this sp. in AZ.

*MELICA IMPERFECTA* TRIN. (POACEAE).—Mohave Co., W side of Black Mts., ca. 10 km N of Oatman, T20N R20W sect. 23 NW¼, in rock crevices of canyon wall, 921 m, 22 Apr 1986, *Butterwick 8892, 8899, 8900, 8989* (ASU, CAS).

*Previous knowledge.* Known from N-cent. through S CA, Baja California, and Baja California Sur, MEX.

*Significance.* First records of this sp. in AZ.—MARY BUTTERWICK, Department of Botany, California Academy of Sciences, San Francisco, CA 94118.



## COMMENTARY

### POINTS OF VIEW:

#### ON THE MODERN DEATH OF DAVID DOUGLAS

David Douglas (1798–1834) is one of the best known nineteenth century botanical explorers of the American West. His exploits have been told in a myriad of books, articles, and television programs. His death in a bull pit on the Hawaiian Islands has long been regarded as a tragedy. In the Pacific states, his name lives. Rivers, counties, and an array of flowering plants and animals carry his name, and the West's single most important lumber tree, Douglas-fir, is a constant reminder that he was a part of our past.

Unfortunately, in the new Jepson's flora, the name of David Douglas is about to disappear.

Botanical editors of various journals and floras, and I mention the Jepson flora only as an example, are reducing author citations to a few letters of print that, they argue, tell us nothing but if discarded can significantly reduce costs. On the latter point they are right. By ridding us of Douglas' name, to mention only one, the space saved will obviously have a profound effect on the ultimate purchase price of any book.

Not all of the fault is that of editors who have read Article 46 of the *International Code of Botanical Nomenclature* (Greuter 1988) and found that *ex* and *in* can be dropped if desired. Many taxonomists use the two terms incorrectly, inconsistently, or, perhaps in a simplistic desire to "simplify nomenclature," just do not bother.

The term *in* is to be used when a name of a taxon and its description or diagnosis are supplied by one author but published *in* the work of another (Art. 46.2). In this case the first author proposed, prepared, and knowingly published a scientific name, but that name appeared *in* a publication that has the name of a second person as its author. The term *ex* is to be used when a name of a taxon proposed by one person is published for them by a second person (Art. 46.3). In this case the second person took a name *from* (*ex*) the first person and prepared and published it typically without the knowledge of the first person because that individual was not in a position to publish.

One can think of *in* as a worker's name in combination with the literary citation (the book's or journal's title), while *ex* is a designation of a combination of two workers' names without any reference to the place of publication. It is because *in* can be regarded as a part of the literature citation that some feel it should be used only when presenting a full citation, such as *Oxytropis viscida* Nutt. *in* Torr. & A. Gray, Fl. N. Amer. 1:341. 1838, but not when the bi- or trinomial stands alone: *O. viscida* Nutt., not *O. viscida* Nutt. *in* Torr. & A. Gray. It is anticipated that one or more proposals will be presented at the next Botanical Congress to modify or delete Art. 46.2.

Nonetheless, the use of *in*, even without a full literary citation, can be useful.

Bentham (1856) contributed the treatment of the tribe Eriogoneae to de Candolle's *Prodromus*. In that treatment, Bentham published several new species, one of them being *Eriogonum douglasii* Benth. *in* A. DC., Prodr. 14:9. 1856. The *Code* (Art. 46.2) allows one to drop the literary citation, "*in* A. DC.", and use just *E. douglasii* Benth.

There is considerable information in the full author citation and it is particularly so in this case as Bentham published new species of *Eriogonum* in several different books and articles. He proposed *E. angulosum* Benth., Trans. Linn. Soc. London 17: 406. 1836, a journal. He also published *E. gracile* Benth. *in* Hinds, Bot. Voy. Sulphur 46. 1844, a section in a book, and *E. parviflorum* Sm. *in* Rees var. *crassifolium* Benth., Pl. Hartw. 333. 1857, a book he wrote himself. By adding the literary reference to the author's name it is often (but not always) immediately obvious where the name



was published. Thus, one can turn directly to that source without having to consult Gray Card Index, *Index kewensis*, the monographic or revisionary literature, or some of the more sophisticated floras where such information can be found.

Douglas' untimely death meant that the bulk of his collections, for which he had provided names and in some instances descriptions, had to be prepared for publication by others. Douglas was greatly respected by his contemporaries and many of them (Hooker, Lindley, Bentham to mention a few) saw to it that his new species were published for him.

These authors did not have to credit Douglas with his own discoveries, after all he was dead; they could have taken his scientific names and descriptions and published them under their own authorships without any reference to their friend.

But these men chose not to do that.

Instead they acknowledged the man who walked across a continent in search of plants, who traveled around the globe to find novelties to remind the intellectual world of the diversity of living things, and who braved the elements of the Pacific Coast to collect seeds and specimens of an unknown flora.

And now some want to strip that acknowledgment and honor away? And yes, I say emphatically, "acknowledgment and honor." There are those who say such emotionalism is not a part of nomenclature, and to express such is foolish. So be it. I am foolish. But does the lack of emotion somehow change history?

The *Code* says that if one wishes to shorten an author citation it can be done by restricting the authorship to the person who actually published the name. Thus, *Eriogonum nudum* Douglas *ex* Benth. would be reduced to just *E. nudum* Benth.

Is that how Bentham published the name?

Is it possible that Bentham did not wish to acknowledge the contribution of his dead colleague?

I say it again emphatically and emotionally—NO!

And the practice of acknowledging the efforts of others is not something that characterizes the distant past. Consider: *Carphochaete macrocephala* (Paray) Grashoff *ex* Turner & Kerr, *Pl. Syst. Evol.* 151:86. 1985; *Adenopodia patens* (Hook. & Arnold) Dixon *ex* Brenan, *Kew Bull.* 41:80. 1986; or *Cologania cordata* Fearing *ex* McVaugh, *Fl. Nov.-Galic.* 5:356. 1987.

So why should editors take it upon themselves to wrench from the written works of decent men their stated desires?

To be sure there is no simple answer and editors are certainly not the only obstacle. Botanical authors must take the time to learn the botanical literature; to read and understand what is in *Taxonomic Literature—II* (Stafleu and Cowan 1976–1988); and to take the time to go back and look up original publications rather than depend upon secondary sources. Even if one wishes to ignore full citations of authorship, and cite only the validating author or the author who supplied the description or diagnosis, it is still necessary to carefully evaluate the literature.

When Nuttall returned to England, he sent to John Torrey and Asa Gray a manuscript, along with some specimens, containing descriptions of 340 new genera and species he found mainly in the West. These were incorporated into Torrey and Gray's *A flora of North America*. Most of the names and descriptions were taken directly from Nuttall's manuscript and may be so noted by the use of quote marks. The authorship of such names is "Nutt. *in* Torr. & A. Gray." In other instances, Torrey and Gray used Nuttall's name, but augmented or modified his description with additional information sometimes taken from other collections. The authorship of these names is "Nutt. *ex* Torr. & A. Gray."

Thus, it is *Arabis puberula* Nutt. *in* Torr. & A. Gray, *Fl. N. Amer.* 1:82. 1838, or *Streptanthus virgatus* Nutt. *ex* Torr. & A. Gray, *Fl. N. Amer.* 1:76. 1838, depending upon the way the name was published. The same is true of new combinations: *Nasturtium curvisiliqua* (Hook.) Nutt. *ex* Torr. & Gray, *Fl. N. Amer.* 1:73. 1838. Sometimes species in a single genus were published both ways: *Cercocarpus ledifolius*



Nutt. *ex* Torr. & Gray, Fl. N. Amer. 1:427. 1840, and *C. betuloides* Nutt. *in* Torr. & Gray, Fl. N. Amer. 1:427. 1840.

Looking at the most recent flora of California (Munz 1959) one finds that the use of *ex* and *in* as they relate to Nuttall's names in Torrey and Gray's *Flora* is not always consistent. Munz correctly cited the authorship of *Paeonia californica* and *Phoenicaulis cheiranthoides* as Nutt. *in* Torr. & Gray, but he erred when he gave the authorships of *Delphinium depauperatum* and *Thysanocarpus laciniatus* as Nutt. *ex* Torr. & Gray (it should be *in*) and in his citation of *Sida californica* and *S. oregana* as Nutt. *in* Torr. & Gray (it should be *ex*).

Clearly, we as authors of floras and especially as monographers have a responsibility to do our nomenclatural work carefully. If the primary workers fail, how can we expect editors to have any choice but to reduce citations to a single element? But a word of caution: editors cannot just simply red line the "*in* Torr. & Gray" from a Nuttall name because of the possibility it may not be correct.

Some individuals, editors and monographers alike, may believe that author citations are just so much bother and will not make any effort to determine correct authorships. This sign of intellectual laziness should not be tolerated. If an author is going to include any author citations, every effort should be made to get them right!

Many and perhaps most may feel that the sole purpose of an author citation is to give precision to the scientific name. For such individuals to ascribe importance, as I do, to historical facts—and especially emotional facts relating to death or failed accomplishments—is equivalent to loading unnecessary baggage onto the system. Yet, who is more "precise," one who gives the full citation, or one who shortens it?

It is estimated that David Douglas found some 500 new species in California. The majority he never saw in print. He published a few species during his lifetime, so his name will remain as a botanical author in Jepson's flora associated with such notable species as *Pinus lambertiana* Douglas, Trans. Linn. Soc. London 15:500. 1827, sugar pine, and *Ribes cerneum* Douglas, Trans. Hort. Soc. London 7:512. 1830, squaw currant. But consider the scientific names to which "Douglas" has long been associated that must now be ripped asunder in the name of "cost savings."

Do the following scientific names and authorships look right? This is how they will appear in the new Jepson flora: *Pinus contorta* Loud., *P. monticola* D. Don, *P. ponderosa* Lawson, and *P. sabiniana* D. Don.

Can one really feel comfortable with *Paeonia brownii* Hook., *Mentzelia laevicaulis* (Hook.) Torr. & A. Gray or *Mimulus cardinalis* Hook.?

Consider the havoc in *Lupinus*! *Lupinus albicaulis* Hook., *L. arbustus* Lindl., *L. laxiflorus* Lindl., *L. lepidus* Lindl., *L. leucophyllus* Lindl., *L. littoralis* Lindl., *L. micranthus* Lindl., *L. rivularis* Lindl., *L. sabinii* Hook., *L. succulentus* Koch, *L. sulphureus* Hook., *L. tenellus* G. Don. At one time Douglas' name was associated with each of these species.

And just think of the author changes that will have to occur elsewhere: *Potentilla gracilis* Hook., *Astragalus lentiginosus* Hook., *Garrya elliptica* Lindl., *Cryptantha flaccida* (Lehm.) E. Greene, *Castilleja miniata* Hook., *Penstemon procerus* Graham, *Penstemon speciosus* Lindl., *Cypripedium montanum* Lindl., *Epipactis gigantea* Hook.

And think of the losses in *Calochortus*. Douglas' name would be lost from *C. albus*, *C. luteus*, *C. pulchellus*, *C. splendens*, and *C. venustus* although it would remain on the two species of the genus he published prior to his death, *C. macrocarpus* and *C. nitidus*.

Is this right? Does the modern death of David Douglas truly reflect the will of a botanical community that has long honored those who have worked to make systematic knowledge available?

How many hundreds if not thousands of authorships will have to be changed? If the editors of the Jepson flora have their way, and the trend extends significantly beyond this publication, we will see the editorial death of numerous individuals who have contributed to the history of botanical explorations and discoveries.



Then there is the confusion factor. Sophisticated and scholarly regional and local floras in California will continue to use full author citations so that those in the new Jepson flora will be markedly different from those in other treatments.

I say the loss of knowledge, of precision, and, yes, the privilege of acknowledging and honoring another by the use of that person's name and the term "*ex*" are not worth the few letters of saved spaces in an occasional line of print.

Let David Douglas live!

#### LITERATURE CITED

- GREUTER, W. (ed.). 1988. International code of botanical nomenclature. *Regnum Veg.* 118:1-328.
- MUNZ, P. A. 1959. A California flora. Univ. California Press, Berkeley.
- STAFLEU, F. A. and R. S. COWAN. 1976-1988. Taxonomic literature—II. *Regnum Veg.* 94:1-1136. 1976; 98:1-991. 1979; 105:1-980. 1981; 110:1-1214. 1983; 112:1-1066. 1985; 115:1-926. 1986; 116:1-653. 1988.
- JAMES L. REVEAL, Department of Botany, University of Maryland, College Park, MD 20742-1815.

## ANNOUNCEMENTS

### NEW PUBLICATIONS

- MICKEL, J. T. and J. M. BEITEL, Pteridophyte flora of Oaxaca, Mexico, *Memoirs of the New York Botanical Garden*, vol. 46, pp. [i-ii], 1-568, 15 Jul 1988, ISSN 0071-5794, ISBN 0-89327-323-6, \$94.85 U.S., \$96.80 foreign, postpaid (from Scientific Publications Office, the New York Botanical Garden, Bronx, NY 10458-5126). [On 102 gen., 690 spp., 65 new; A. R. Smith's 1981 Pteridophyte flora of Chiapas (*Fl. Chiapas* 2: 1-370) treated 609 spp., ca. 150 not found in Oaxaca. The two state floras thus have some 84% of the over 1000 pteridophyte spp. in Mexico.]
- MILL, S. W., D. P. GOWING, D. R. HERBST, and W. L. WAGNER, *Indexed bibliography on the flowering plants of Hawai'i*, University of Hawaii Press, 2840 Kolowalu St., Honolulu, Hawaii 96822, 3 Oct 1988, vi, 214, [1] pp., unillus., ISBN 0-8248-1169-0 (hardbound), \$25.00. [Indexed biblio. of 3257 entries. Contents: intro; definitions of subject categories; biblio.; subject index (29 categories); indices to plant and place names. A superb biblio. forming the basis for Wagner, Herbst, and S. H. Sohmer's *Manual of the flowering plants of Hawaii* (in press).]
- PARK, C.-W., Taxonomy of *Polygonum* section *Echinocaulon* (Polygonaceae), *Memoirs of the New York Botanical Garden*, vol. 47, pp. i-ii, 1-82, 20 Jul 1988, ISSN 0071-5794, ISBN 0-89327-329-5, \$21.45 U.S., \$22.60 foreign, postpaid (for address see entry for Mickel & Beitel). [On 21 spp. (1 comb. nov.), incl. morphology, flavonoid chemistry, geography.]



## SUBSCRIPTIONS—MEMBERSHIP

Membership in the California Botanical Society is open to individuals (\$22 per year; students \$12 per year for a maximum of seven years). Members of the Society receive *MADROÑO* free. Family memberships (\$25) include one five-page publishing allotment and one journal. Emeritus rates are available from the Corresponding Secretary. Institutional subscriptions to *MADROÑO* are available (\$30). Membership is based on a calendar year only. Applications for membership (including dues), orders for subscriptions, and renewal payments should be sent to the Treasurer. Requests and rates for back issues, changes of address, and undelivered copies of *MADROÑO* should be sent to the Corresponding Secretary.

## INFORMATION FOR CONTRIBUTORS

Manuscripts submitted for publication in *MADROÑO* should be sent to the editor. All authors must be members, and membership is prerequisite for review.

Manuscripts and review copies of illustrations must be submitted in triplicate for all articles *and* short items intended for NOTES AND NEWS. Follow the format used in recent issues for the type of item submitted and allow ample margins all around. All manuscripts **MUST BE DOUBLE SPACED THROUGHOUT**. For articles this includes title (all caps, centered), author names (all caps, centered), addresses (caps and lower case, centered), abstract, text, acknowledgments, literature cited, tables (caption on same page), and figure captions (grouped as consecutive paragraphs on one page). Order parts in the sequence listed ending with figures, and number each page. Do not use a separate cover page, “erasable” paper, or footnotes. Manuscripts prepared on dot matrix printers may not be considered. Table captions should include all information relevant to tables. All measurements should be in metric units.

Line copy illustrations should be clean and legible, proportioned (including captions) to the *MADROÑO* page, and designed for reduction to  $\frac{2}{3}$  original size. Scales should be included in figures, as should explanation of symbols, including graph coordinates. Symbols smaller than 1 mm after reduction are not acceptable. Maps must include latitude and longitude references. Halftone copy should be designed for reproduction at actual size. In no case should original illustrations be sent prior to the acceptance of a manuscript. When needed they should be mounted on stiff cardboard and sent flat. No illustrations larger than 22 × 28 cm will be accepted.

Presentation of nomenclatural matter (accepted names, synonyms, typification) should follow the format used for *Rhus integrifolia* in *MADROÑO* 22:288. 1974. Institutional abbreviations in specimen citations should follow Holmgren, Keuken, and Schofield, *Index Herbariorum*, 7th edition. Abbreviations of serial titles should be those in *Botanico-Periodicum-Huntianum* (Lawrence et al., 1968, Hunt Botanical Library, Pittsburgh). If the correct abbreviation cannot be determined, the full serial title should be used. Titles of books should be given in full, together with the place and date of publication, publisher, and edition, if other than the first.

All members of the California Botanical Society are allotted five free pages per volume in *MADROÑO*. Joint authors may split the full page number. Beyond that number of pages a required editorial fee of \$65.00 per page will be assessed. The purpose of this fee is not to pay directly for the costs of publishing any particular paper, but rather to allow the Society to continue publishing *MADROÑO* on a reasonable schedule, with equity among all members for access to its pages. Printer's fees for illustrations and typographically difficult material @ \$35.00 per page (if their sum exceeds 30 percent of the paper) and for author's changes after typesetting @ \$4.50 per line will be charged to authors.

At the time of submission, authors must provide information describing the extent to which data in the manuscript have been used in other papers that are published, in press, submitted, or soon to be submitted elsewhere.





CALIFORNIA BOTANICAL SOCIETY



3

# MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

## Contents

|  |               |
|--|---------------|
| EFFECT OF <i>QUERCUS DOUGLASII</i> (FAGACEAE) ON HERBACEOUS UNDERSTORY ALONG A RAINFALL GRADIENT<br><i>Mitchel P. McClaran and James W. Bartolome</i>  | 141           |
| EFFECTS OF VARYING FIRE REGIMES ON ANNUAL GRASSLANDS IN THE SOUTHERN SIERRA NEVADA OF CALIFORNIA<br><i>David J. Parsons and Thomas J. Stohlgren</i>    | 154           |
| PHYTOGEOGRAPHICAL NOTES ON ACIDOPHILOUS <i>CLADONIA</i> SPECIES IN CALIFORNIA<br><i>Samuel Hammer</i>  | 169           |
| A NOTE ON THE GERMINATION AND ESTABLISHMENT OF <i>PHORADENDRON CALIFORNICUM</i> (VISCACEAE)<br><i>Job Kuijt</i>  | 175           |
| REDUCTION IN LIGHT REFLECTANCE OF LEAVES OF <i>ENCELIA DENSIFOLIA</i> (ASTERACEAE) BY TRICHOME WETTING<br><i>Daniel F. Harrington and Curtis Clark</i> | 180           |
| THE <i>ARISTIDA CALIFORNICA-GLABRATA</i> COMPLEX (GRAMINEAE)<br><i>John R. Reeder and Richard S. Felger</i>  | 187           |
| A NEW SPECIES OF <i>SIPHONOGLOSSA</i> (ACANTHACEAE) AND SOME INFRAGENERIC TRANSFERS<br><i>Richard A. Hilsenbeck</i>                                    | 198           |
| SEGREGATION OF <i>HASTINGSIA SERPENTINICOLA</i> SP. NOV. FROM <i>HASTINGSIA ALBA</i> (LILIACEAE: ASPHODELEAE)<br><i>Rudolph W. Becking</i>             | 208           |
| NOTES  |               |
| <i>ISOPYRUM STIPITATUM</i> A. GRAY (RANUNCULACEAE) IN THE WILLAMETTE VALLEY, OREGON<br><i>Edward R. Alverson</i>                                       | 217           |
| NOTEWORTHY COLLECTIONS   |               |
| BRITISH COLUMBIA   | 153           |
| CALIFORNIA   | 207           |
| MONTANA  | 174           |
| OREGON   | 207           |
| COMMENTARY   |               |
| POINTS OF VIEW: RESPONSE TO REVEAL<br><i>James C. Hickman</i>  | 218           |
| REVIEWS  | 219           |
| ANNOUNCEMENTS  | 168, 197, 218 |



MADROÑO (ISSN 0024-9637) is published quarterly by the California Botanical Society, Inc., and is issued from the office of the Society, Herbarium, Life Sciences Building, University of California, Berkeley, CA 94720. Subscription rate: \$30 per calendar year. Subscription information on inside back cover. Established 1916. Second-class postage paid at Berkeley, CA, and additional mailing offices. Return requested. POSTMASTER: Send address changes to James R. Shevock, Botany Dept., California Academy of Sciences, San Francisco, CA 94118.

*Editor*—DAVID J. KEIL  
Biological Sciences Department  
California Polytechnic State University  
San Luis Obispo, CA 93407

*Board of Editors*

Class of:

- 1989—FRANK VASEK, University of California, Riverside, CA  
BARBARA ERTTER, University of California, Berkeley, CA  
1990—STEVEN TIMBROOK, Ganna Walska Lotusland Foundation, Montecito, CA  
THOMAS R. VAN DEVENDER, Arizona-Sonora Desert Museum, Tucson, AZ  
1991—JAMES HENRICKSON, California State University, Los Angeles, CA  
WAYNE R. FERREN, JR., University of California, Santa Barbara, CA  
1992—BRUCE A. STEIN, The Nature Conservancy, Washington, D.C.  
WILLIAM L. HALVORSON, Channel Islands National Park, Ventura, CA  
1993—JON E. KEELEY, Occidental College, Los Angeles, CA  
RHONDA L. RIGGINS, California Polytechnic State University, San Luis Obispo, CA

---

CALIFORNIA BOTANICAL SOCIETY, INC.

OFFICERS FOR 1989-90

- President:* ROBERT W. PATTERSON, Biological Sciences Department, San Francisco State University, San Francisco, CA 94132  
*First Vice President:* NIAL F. MCCARTEN, Department of Integrative Biology, University of California, Berkeley, CA 94720  
*Second Vice President:* MARY L. BOWERMAN, 970 Second Street, Lafayette, CA 94549  
*Recording Secretary:* RODNEY G. MYATT, Department of Biological Sciences, San Jose State University, San Jose, CA 95192  
*Corresponding Secretary:* BARBARA ERTTER, University Herbarium, University of California, Berkeley, CA 94720  
*Treasurer:* MONA BOURELL, Department of Botany, California Academy of Science, San Francisco, CA 94118  
*Financial Officer:* BARRETT ANDERSON, Department of Botany, California Academy of Science, San Francisco, CA 94118

The Council of the California Botanical Society consists of the officers listed above plus the immediate *Past President*, JOHN STROTHER, University Herbarium, University of California, Berkeley, CA 94720; the *Editor* of MADROÑO; three elected *Council Members*: JAMES SHEVOK, Department of Botany, California Academy of Science, San Francisco, CA 94118; ELIZABETH MCCLINTOCK, University Herbarium, University of California, Berkeley, CA 94720; BRUCE PAVLIK, Department of Biology, Mills College, Oakland, CA 94613; and a *Graduate Student Representative*, JAMES D. MOREFIELD, Rancho Santa Ana Botanic Garden, Claremont, CA 91711.

|   |
|---|
| THIS PUBLICATION IS PRINTED ON ACID-FREE PAPER. |
|---|



# EFFECT OF *QUERCUS DOUGLASII* (FAGACEAE) ON HERBACEOUS UNDERSTORY ALONG A RAINFALL GRADIENT

MITCHEL P. McCLARAN

Division of Range Resources,  
School of Renewable Natural Resources,  
University of Arizona, Tucson, AZ 85721

JAMES W. BARTOLOME

Department of Forestry and Resource Management,  
University of California, Berkeley, CA 94720

## ABSTRACT

Variation in effect of approximately 50% *Quercus douglasii* (blue oak) cover on herbaceous understory biomass and composition was studied along a rainfall gradient between five sites. Biomass and composition were compared between understory and adjacent open grassland at each site to evaluate changes in canopy effect along the gradient. Biomass was measured at the time of greatest standing biomass (PEAK) in 1986 and 1987. Composition was measured at PEAK 1986. Annual rainfall was above average in 1985–1986, and below average in 1986–1987. In both years PEAK biomass was greater in grassland than understory at sites with  $>50$  cm yr<sup>-1</sup> average rainfall, and no difference was apparent at sites with  $<50$  cm yr<sup>-1</sup> rainfall. Variation in species composition between grassland and understory was independent of rainfall gradient. Differences in individual species presence and abundance between grassland and understory were found at all sites. We conclude that variation in canopy effect on biomass resulted from changes in relative production between understory and open grassland, not from differences in relative composition.

Winter deciduous *Quercus douglasii* Hook. & Arn. (blue oak) forms a patchy canopy over and within a continuous annual herbaceous layer on more than a million hectares in California (McClaran and Bartolome 1989). Average rainfall in blue oak woodland varies geographically from 30 to 100 cm yr<sup>-1</sup> (Griffin 1977). In high rainfall areas understory biomass was lower than open grassland (Bartolome 1986; Jansen 1987), and understory biomass increased after thinning or removal of oak canopy (Johnson et al. 1959; Heady and Pitt 1979; Kay 1987). In low rainfall areas understory biomass was greater than in open grassland (Duncan and Reppert 1960; Holland 1980). Composition differences between grassland and understory were reported for several sites (Heady and Pitt 1979; Holland 1980; Bartolome 1986; Jansen 1987). Because *Q. douglasii* cover was not constant among these study sites, relative influence of rainfall and tree cover on herbaceous biomass and composition cannot be interpreted.



In general, differences between understory and grassland composition have been attributed to negative competition effects or positive site modification effects (e.g., Parker and Muller 1982; Yavitt and Smith 1983; Schott and Pieper 1985). Biomass differences between understory and grassland also have been attributed to these positive and negative effects. Examples of positive effects described for relatively xeric areas (e.g., Tiedemann and Klemmedson 1977; Patten 1978), contrast with negative effects in mesic regions (e.g., Halls and Schuster 1965; Jameson 1967; Ford and Newbould 1977). Negative effects of light and water competition were suggested in tree-grass models (Walker et al. 1981; McMurtie and Wolf 1983) and the interpretation of empirical biomass data (Knoop and Walker 1985).

The suggestion that species interactions vary along environmental gradients (Begon et al. 1986) provides a framework to organize the diversity of canopy effects by *Quercus douglasii*. We used this framework to identify our objective and generate a null hypothesis. To evaluate effects of rainfall and *Q. douglasii* canopy on herbaceous understory, we used the null hypothesis that the effect of 50% *Q. douglasii* canopy on the similarity of grassland and understory biomass and composition does not vary along a rainfall gradient.

## METHODS

*Study sites.* We selected five sites along an average annual rainfall gradient of 40 to 90 cm yr<sup>-1</sup> (Tables 1 and 2, Fig. 1). Livestock had grazed all sites each year for the last five years prior to 1985. Slopes on all sites were less than 15 percent with either a west or a south aspect.

At each site we sampled herbaceous biomass and composition under three canopies and their adjacent open grassland areas. All canopies consisted of three to five *Quercus douglasii* projecting approximately 50% cover over 100–200 m<sup>2</sup>. Trees were 7–10 m tall, 30–60 cm in diameter at 1.35 m height, and 2–5 m apart. The sample canopies were randomly selected from 5–6 available canopies with the above characteristics at each site. To study ungrazed herbaceous vegetation we randomly placed two pair (pair = one understory and one grassland) of 1-m<sup>2</sup> pyramidal cages (Frishnecht and Conrad 1965) in each of the three understory and grassland areas per site.

*Biomass.* We estimated live herbaceous biomass at the time of greatest standing biomass (PEAK) in early to late May 1986 and 1987 because phenology varies with latitude. The estimates were made within livestock exclosure cages by weighing vegetation clipped in a 0.0625-m<sup>2</sup> plot to 1 cm height, and dried at 65°C for 48 hr. Cages were again randomly located after PEAK sampling in 1986 to accommodate 1987 sampling.



TABLE 1. LOCATION AND CHARACTERISTICS OF *QUERCUS DOUGLASII* CANOPY STUDY SITES. <sup>1</sup> Data from Gowans (1958), Herbert and Begg (1969), Kimchang (1965), and Lindsey (1974, 1983). <sup>2</sup> Data from Stangenberger and Mallory (1981).

| Site (ownership)                         | Longitude | Latitude | Elevation (m) | Soil texture <sup>1</sup> | Soil family <sup>2</sup>            |
|--|-----------|----------|---------------|---------------------------|-------------------------------------|
| Hopland (Univ. Calif. Expt. Sta.)        | 39°N      | 123°5'W  | 370           | silt loam                 | ultic haploxeroll                   |
| Sierra (Univ. Calif. Expt. Sta.)         | 39°16'N   | 121°17'W | 400           | rocky loam                | mollic haploxeralf                  |
| San Felipe (private ranch)               | 37°15'N   | 121°37'W | 850           | loam                      | lithic xerothent                    |
| San Joaquin (U.S. For. Serv. Expt. Sta.) | 37°10'N   | 119°35'W | 370           | coarse sandy loam         | mollic haploxeralf                  |
| Sinton (private ranch)                   | 35°30'N   | 120°20'W | 460           | coarse loam               | typic haploxeralf-pachic argixeroll |



TABLE 2. CUMULATIVE SEASONAL RAINFALL AT STUDY SITES DURING 1985–1986 AND 1986–1987, AND LONG-TERM AVERAGE. <sup>1</sup> Station records for Hopland, Sierra, and San Joaquin; nearest National Atmospheric and Oceanic Administration (NAOA) station, Mt. Hamilton for San Felipe and Paso Robles for Sinton. <sup>2</sup> Only trace amounts of rainfall occur between May and September in this Mediterranean climate.

| Site <sup>1</sup> | Rainfall (cm) |      |           |                    |           |           |                           |           |           | Length<br>of<br>record |
|-------------------|---------------|------|-----------|--------------------|-----------|-----------|---------------------------|-----------|-----------|------------------------|
|                   | 1 Sep–30 Nov  |      |           | 1 Sep–28 Feb       |           |           | 1 Sep–30 Apr <sup>2</sup> |           |           |                        |
|                   |               |      |           |                    |           |           |                           |           |           |                        |
|                   | 1985          | 1986 | $\bar{x}$ | 1985–1986–<br>1986 | 1986–1987 | $\bar{x}$ | 1985–1986–<br>1986        | 1986–1987 | $\bar{x}$ |                        |
| Hopland           | 26.2          | 7.8  | 21.1      | 92.5               | 42.0      | 73.8      | 112.0                     | 59.3      | 92.6      | 34 yr                  |
| Sierra            | 21.6          | 8.0  | 18.2      | 67.1               | 34.6      | 55.2      | 84.8                      | 48.1      | 70.6      | 25 yr                  |
| San Felipe        | 15.9          | 9.5  | 10.1      | 46.7               | 25.2      | 39.7      | 61.8                      | 35.7      | 52.7      | 106 yr                 |
| San Joaquin       | 14.9          | 2.3  | 8.7       | 41.4               | 19.5      | 33.6      | 54.3                      | 27.5      | 46.3      | 53 yr                  |
| Sinton            | 3.8           | 2.0  | 5.9       | 29.2               | 8.6       | 27.5      | 35.1                      | 17.6      | 41.8      | 101 yr                 |

We analyzed PEAK biomass with a 3-way analysis of variance (ANOVA) to assess year, site, and canopy effects. When main effects or interactions were significant, we employed Duncan’s multiple range test to determine year, site, and canopy differences (Steel and Torrie 1980).

*Composition.* We estimated aerial cover by species in each cage immediately prior to 1986 PEAK biomass sample. Estimates were made by recording the first species hit when lowering a fine-tipped metal pin 100 times per cage. Pins were mounted in a ten pin point-frame (Heady and Rader 1958) that was independently placed in ten different locations per cage to amass 100 hits. Taxonomic nomenclature follows Munz (1968). Bareground was recorded when the pin did not hit vegetation. To assess site and canopy effects on total plant cover, grass and forb cover, and cover of species that were present on all five sites we used a 2-way ANOVA. When main effects or interactions were significant, we employed Duncan’s multiple range test to determine year, site, and canopy differences (Steel and Torrie 1980). We normalized cover data with an angular (arcsin) transformation before ANOVA and Duncan’s analysis (Steel and Torrie 1980).

We used a cover-weighted similarity index to compare species composition in understory and grassland between study sites. Similarity was estimated with a cover weighted modification of Sorensen’s (1948) similarity index (SI) that Barbour et al. (1987) described as:

$$SI = \left( \sum_{\text{all } i} 2 C_i \right) / (A + B)$$





FIG. 1. Location of five study sites in California.

where A is total percent cover in stand A, B is total percent cover in stand B, and C is the lowest percent cover of species i from either stand A or B. To estimate between site change in species composition along the gradient we calculated a similarity index between adjacent study sites for both understory (UNDER) and open grassland (OPEN). Rogers (1980) used this technique to describe composition changes between adjacent sites along a gradient.

This research design stresses the difference between grassland and understory within each site, and compares these within-site differences among sites to describe a change in canopy effect along a rainfall gradient. The between-site differences in absolute grassland or absolute understory biomass and composition that also are available from this research design are mostly expected and less germane to our study objective. We chose a relatively small sample size of six plots from three canopies and grasslands at each site to enable completion of biomass and composition sampling at a site in one day. This pace allowed us to minimize phenologic differences among sites by sampling adjacent sites on subsequent days. The ANOVA procedures compensate for small sample sizes by requiring greater differences between population means to reach significant differences (Steel and Torrie 1980). We could not complete the composition



sampling in 1987, and we recognize the importance of yearly variability in annual grassland composition (Pitt and Heady 1978). However, we include the 1986 composition data because it reveals interesting relationships between biomass and composition along the rainfall gradient, and it represents unique empirical data for comparison with future work.

## RESULTS

*Biomass.* Significant canopy  $\times$  site, and year  $\times$  site interactions were found for herbaceous biomass at PEAK sampling period from 3-way ANOVA (Table 3). Canopy  $\times$  site interaction shows a change in OPEN biomass relative to UNDER biomass along the gradient: as rainfall increased OPEN biomass exceeded UNDER (Fig. 2). Year  $\times$  site interaction shows less PEAK biomass in 1987 than 1986 at all sites except San Felipe (Fig. 2). Absence of significant canopy  $\times$  year, and site  $\times$  canopy  $\times$  year interactions illustrates the consistency of this pattern between wet and dry years (Table 3), even though absolute biomass values differed between years (Fig. 2).

*Composition.* Fifty-six species were recorded on all five sites combined. Nearly half were found only in grassland or understory; 13 species were recorded only in grassland and 14 species only in understory. A complete species list is available from the senior author. Aerial cover of only seven herbaceous species was present on all of the five sites (Table 4).

*Avena barbata*, *Bromus diandrus*, *Lupinus bicolor*, forb, and total cover varied among sites (Table 5). *Avena barbata* cover was greater at San Felipe and Hopland than at Sinton and San Joaquin. *Bromus diandrus* cover was greater at Sinton than San Felipe, and *L. bicolor* was greater at San Felipe than at Hopland. Forb cover was greater at Sierra and Hopland than at San Joaquin. Total cover was greater at San Felipe and Hopland than at other sites.

*Bromus diandrus*, *Erodium cicutarium*, *Lupinus bicolor*, forb, and total cover varied between grassland and understory (Table 5). *Bromus diandrus* cover was greater under canopy, and the other taxa and taxa groups were greater in grassland.

Significant canopy  $\times$  site interactions were found for *Bromus mollis*, *Festuca megalura*, and grass cover (Table 5). *Bromus mollis* was greater in grassland than understory at all sites except San Joaquin and Sierra. *Festuca megalura* cover was only greater under canopy than in grassland at San Felipe. Understory grass cover was greater than grassland cover at Sierra and San Joaquin.

Similarity of grassland and understory composition between adjacent sites varied along the rainfall gradient (Fig. 3). Similarity index (SI) values for grassland and understory between Hopland, Sierra, and San Felipe were similar. Between San Felipe and San Joaquin



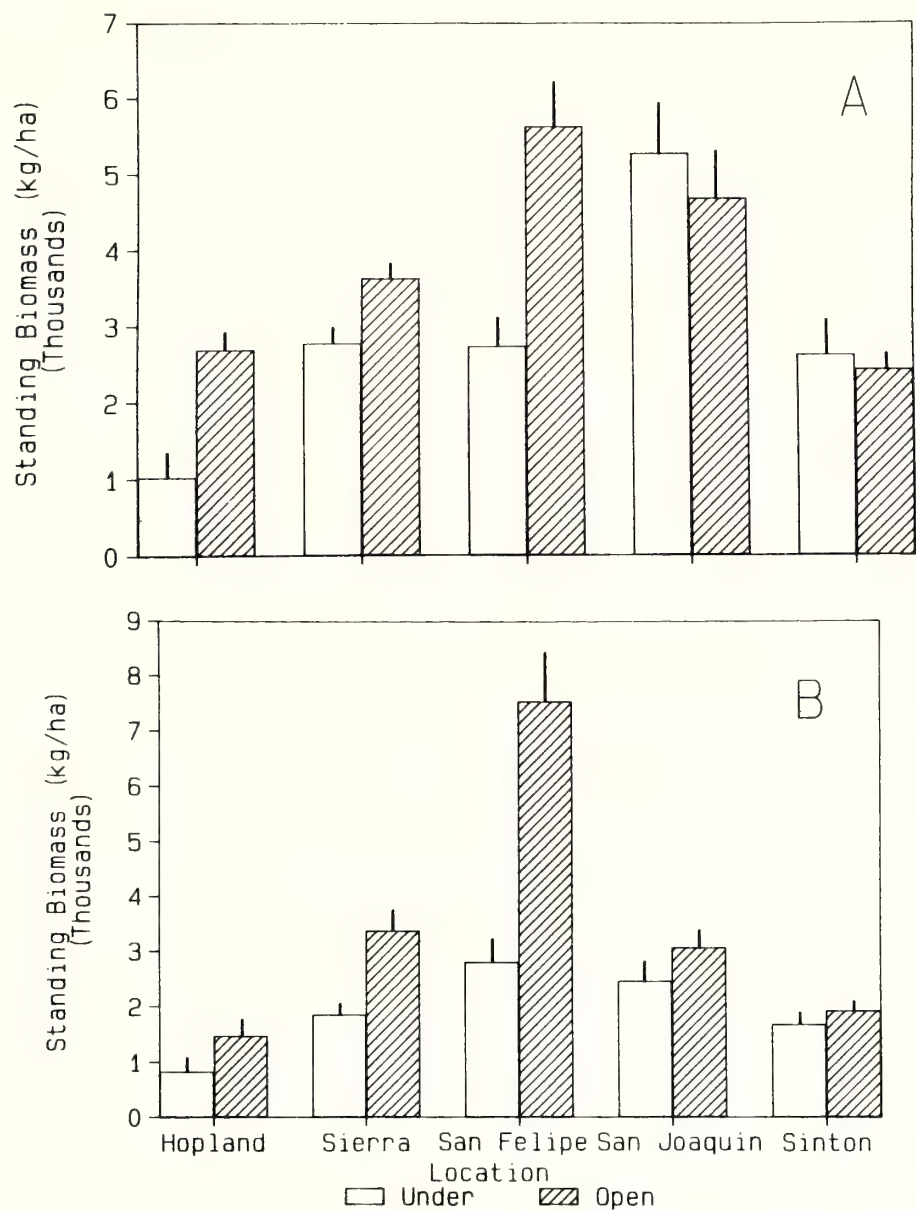


FIG. 2. Understory (open bars) and open grassland (diagonal-hatched bars) standing biomass for five study sites in PEAK 1986 (A) and PEAK 1987 (B). Vertical bars represent  $\pm$ one standard error of the mean.

grassland SI increased while understory decreased. Between San Joaquin and Sinton understory SI increased to a level similar to the grassland.

TABLE 3. PROBABILITY VALUES FOR ANOVA F STATISTIC DESCRIBING SITE, CANOPY, YEAR, AND INTERACTION EFFECTS ON PEAK HERBACEOUS BIOMASS. Significance of single variables is of no consequence if the interaction of these variables is significant.

| Variables and interactions |        |                      |       |                    |                      |                                    |
|----------------------------|--------|----------------------|-------|--------------------|----------------------|------------------------------------|
| Site                       | Canopy | Site $\times$ canopy | Year  | Site $\times$ year | Canopy $\times$ year | Site $\times$ canopy $\times$ year |
| 0.0001                     | 0.0001 | 0.0001               | 0.001 | 0.0001             | 0.09                 | 0.183                              |



TABLE 4. TOTAL AND ABSOLUTE COVER OF COMMON SPECIES AT 1986 PEAK SAMPLING PERIOD FOR UNDERSTORY AND OPEN GRASSLAND AMONG THE FIVE STUDY SITES. Values in parentheses represents one standard error of the mean.

| Species                   | Study sites   |               |               |               |               |               |               |               |               |               |
|---------------------------|---------------|---------------|---------------|---------------|---------------|---------------|---------------|---------------|---------------|---------------|
|                           | Hopland       |               | Sierra        |               | San Felipe    |               | San Joaquin   |               | Sinton        |               |
|                           | Under         | Open          | Under         | Open          | Under         | Open          | Under         | Open          | Under         | Open          |
| <i>Avena barbata</i>      | 5.3<br>(2.2)  | 6.2<br>(2.5)  | 3.5<br>(2.1)  | 4.0<br>(1.4)  | 4.0<br>(1.4)  | 9.5<br>(2.2)  | 1.7<br>(1.3)  | 1.7<br>(1.3)  | 1.5<br>(1.5)  | 1.3<br>(1.3)  |
| <i>Bromus mollis</i>      | 0.7<br>(0.7)  | 12.7<br>(1.0) | 4.7<br>(1.8)  | 10.7<br>(2.5) | 2.7<br>(1.1)  | 17.7<br>(2.5) | 15.3<br>(2.5) | 18.8<br>(5.0) | 2.5<br>(1.9)  | 2.2<br>(2.8)  |
| <i>Bromus diandrus</i>    | 13.5<br>(4.2) | 0.7<br>(0.7)  | 9.3<br>(5.1)  | 0.8<br>(0.7)  | 4.5<br>(1.8)  | 1.8<br>(0.8)  | 12.9<br>(2.9) | 4.5<br>(2.1)  | 21.3<br>(3.4) | 3.0<br>(2.8)  |
| <i>Erodium cicutarium</i> | 0.0<br>(0.0)  | 13.0<br>(6.8) | 0.0<br>(0.0)  | 6.0<br>(1.9)  | 1.0<br>(0.8)  | 12.3<br>(3.1) | 2.8<br>(1.3)  | 16.3<br>(4.2) | 2.8<br>(1.1)  | 8.0<br>(3.3)  |
| <i>Festuca megalura</i>   | 3.7<br>(2.6)  | 0.0<br>(0.0)  | 0.2<br>(0.2)  | 0.5<br>(0.3)  | 5.0<br>(1.9)  | 0.0<br>(0.0)  | 5.2<br>(3.3)  | 4.8<br>(3.1)  | 0.5<br>(0.5)  | 3.3<br>(1.5)  |
| <i>Lupinus bicolor</i>    | 0.0<br>(0.0)  | 0.2<br>(0.2)  | 0.0<br>(0.0)  | 1.0<br>(0.6)  | 0.5<br>(0.5)  | 4.7<br>(1.4)  | 0.0<br>(0.0)  | 2.3<br>(1.5)  | 0.0<br>(0.0)  | 9.0<br>(4.7)  |
| <i>Medicago hispida</i>   | 0.0<br>(0.0)  | 0.7<br>(0.7)  | 0.7<br>(0.3)  | 2.7<br>(1.7)  | 0.5<br>(0.5)  | 0.2<br>(0.2)  | 0.0<br>(0.0)  | 0.2<br>(0.2)  | 1.7<br>(0.8)  | 1.5<br>(1.5)  |
| Forb                      | 20.3<br>(3.5) | 38.8<br>(5.4) | 21.0<br>(3.5) | 38.2<br>(6.2) | 25.3<br>(5.0) | 23.3<br>(4.8) | 6.3<br>(1.7)  | 27.5<br>(4.9) | 13.0<br>(4.0) | 29.0<br>(6.3) |
| Grass                     | 23.7<br>(6.7) | 24.8<br>(2.9) | 43.2<br>(3.3) | 27.2<br>(2.7) | 23.0<br>(4.9) | 33.3<br>(5.0) | 47.8<br>(4.2) | 31.3<br>(3.7) | 36.8<br>(2.2) | 33.7<br>(4.6) |
| Total                     | 44.0<br>(7.5) | 62.0<br>(4.7) | 64.2<br>(1.4) | 65.3<br>(4.1) | 48.3<br>(3.9) | 56.7<br>(1.4) | 54.2<br>(3.0) | 58.8<br>(3.0) | 49.8<br>(3.2) | 62.7<br>(3.8) |



TABLE 5. PROBABILITY VALUES FOR ANOVA F STATISTIC DESCRIBING SITE, CANOPY, AND INTERACTION EFFECTS ON TOTAL AND ABSOLUTE COVER OF COMMON HERBACEOUS SPECIES AND SPECIES GROUPS DURING PEAK SAMPLING PERIOD, 1986. Significance of single variables is of no consequence if the interaction of these variables is significant.

| Species/species groups    | Variables and interactions |        |               |
|---------------------------|----------------------------|--------|---------------|
|                           | Site                       | Canopy | Site × canopy |
| <i>Avena barbata</i>      | 0.01                       | 0.24   | 0.48          |
| <i>Bromus mollis</i>      | 0.001                      | 0.001  | 0.01          |
| <i>Bromus diandrus</i>    | 0.06                       | 0.001  | 0.10          |
| <i>Erodium cicutarium</i> | 0.31                       | 0.001  | 0.50          |
| <i>Festuca megalura</i>   | 0.16                       | 0.32   | 0.22          |
| <i>Lupinus bicolor</i>    | 0.06                       | 0.002  | 0.07          |
| <i>Medicago hispida</i>   | 0.16                       | 0.37   | 0.62          |
| GRASS                     | 0.005                      | 0.076  | 0.01          |
| FORB                      | 0.04                       | 0.001  | 0.12          |
| TOTAL                     | 0.02                       | 0.001  | 0.23          |

DISCUSSION

Variation in similarity of herbaceous biomass in grassland and under approximately 50% *Quercus douglasii* canopy along a rainfall gradient lead to our rejection of the null hypothesis for biomass. Change in similarity occurred at approximately 50 cm yr<sup>-1</sup> average rainfall; similarity in biomass was greater below 50 cm yr<sup>-1</sup>. This pattern was repeated in both wet and dry years. We did not reject the null hypothesis for composition because grassland and understory similarity varied independently of the rainfall gradient.

Neutral canopy effects characterized response of PEAK herbaceous biomass to *Quercus douglasii* at lower rainfall sites. PEAK biomass was not different between grassland and understory at San Joaquin and Sinton. Negative canopy effects characterized response of PEAK herbaceous biomass to *Q. douglasii* at higher rainfall sites. PEAK biomass was higher in grassland than understory at Hopland, Sierra, and San Felipe.

Variation in *Quercus douglasii* effect on herbaceous biomass was assumed in recent mangement guidelines describing optimum stocking levels of oak (Passof et al. 1985). These guidelines suggested 1) reducing tree cover below 50% on sites with > 50 cm average rainfall to increase herbaceous production, and 2) maintaining tree cover at approximately 50% on sites with < 50 cm average rainfall to combine high herbaceous production with oak browse, acorn crops, wildlife habitat, and potential fuelwood. Our results document a shift in understory biomass around a 50% tree cover and 50 cm yr<sup>-1</sup> rainfall intersection. However, our results do not address impacts of tree removal from 50% cover to lower levels, reduction to 50% from higher levels, or unmanipulated oak cover at levels other than 50%.



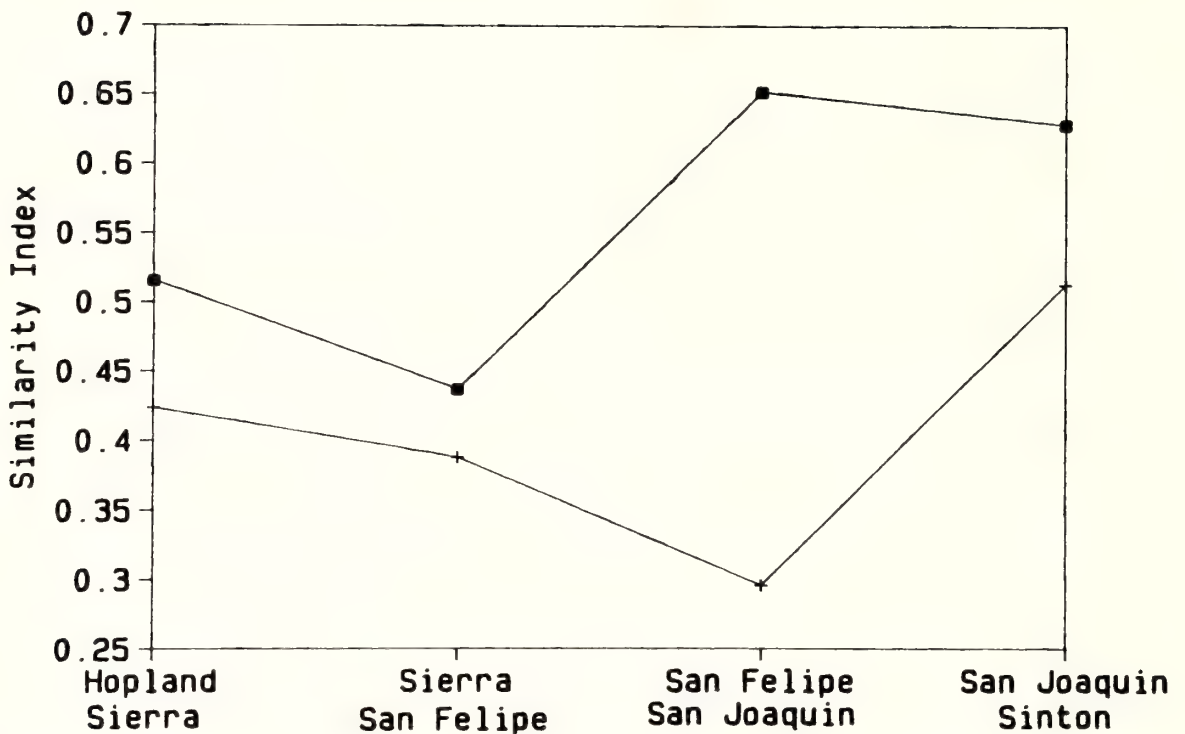


FIG. 3. Similarity of understory (crosses) and open grassland (solid boxes) species composition between adjacent sites along the rainfall gradient.

We suggest that differences in species composition between grassland and understory are independent of the rainfall gradient. This interpretation is supported by canopy effects that are consistently positive or negative throughout the gradient. Nearly half the species were found in only grassland or understory; *Bromus diandrus* cover was greater in understory than grassland; and *Erodium cicutarium*, *Lupinus bicolor*, forb, and total cover were greater in grassland than in understory. Furthermore, there was no gradient related distribution of sites where *Q. douglasii* effect on composition varied from negative to neutral to positive. Understory grass and *Bromus mollis* cover were greater than in grassland at all sites except San Joaquin and Sierra; understory *F. megalura* cover was greater than in grassland only at San Felipe. In addition, the shift from comparable similarity in grassland and understory composition between adjacent high-rainfall sites, to disparity between San Felipe and San Joaquin was not repeated between San Joaquin and Sinton. Because composition was measured only in 1986, interpretations should recognize yearly variation in annual grassland composition (Pitt and Heady 1978). However, relative yearly variation between grassland and understory composition is not known.

Inconsistent trends in biomass and composition similarity between understory and grassland along the gradient suggests that biomass and composition change independently. We propose that the



gradient related effect of *Quercus douglasii* on herbaceous biomass results from changes in relative understory and grassland production, not from changes in relative composition.

We hypothesize that understory production increases relative to grassland in low rainfall areas because *Quercus douglasii* shading improves available soil moisture for herbaceous growth. However, it is probable that *Q. douglasii* ameliorates other potentially limiting factors such as soil nutrients and extreme temperatures in low rainfall areas. Our hypothesis is based on annual grassland production and rainfall relationships. Especially important is maximum production in spring (Pitt and Heady 1978). Where PEAK understory biomass is not lower than that of grassland, we suggest shading by oak foliage prolongs availability of soil moisture in spring enabling understory biomass to reach grassland levels despite negative effects of light reduction. If this hypothesis has merit then availability of soil moisture in late spring will be greater under 50% *Q. douglasii* canopy than grassland only on sites with  $<50 \text{ cm yr}^{-1}$  average rainfall.

We conclude that the effect of 50% *Quercus douglasii* canopy on herbaceous understory biomass does vary along a rainfall gradient, but species composition does not. Above  $50 \text{ cm yr}^{-1}$  average rainfall understory biomass is less than open grassland, but below  $50 \text{ cm yr}^{-1}$  there is no difference in biomass.

#### ACKNOWLEDGMENTS

This research was funded in part by the California Department of Forestry. A. Dennis, D. Duncan, J. Dunne, L. Huntsinger, N. McDougald, A. Murphy, D. Springsteen, and W. Weitkamp assisted in plot location and sampling; and M. Blumler, C. Gonzales, B. Roundy, and E. L. Smith carefully reviewed earlier versions of this manuscript.

#### LITERATURE CITED

- BARBOUR, M. G., J. H. BURK, and W. D. PITTS. 1987. Terrestrial plant ecology, 2nd ed. Benjamin/Cummings Publ. Co., Menlo Park, CA.
- BARTOLOME, J. W. 1986. Herbaceous productivity in oak woodland. Trans. Western Sect. Wildlife Soc. 22:112–116.
- BEGON, M., J. C. HARPER, and C. R. TOWNSEND. 1986. Ecology: individuals, populations, and communities. Sinauer Associates Inc., Sunderland, MA.
- DUNCAN, D. A. and J. N. REPERT. 1960. A record drought in the foothills. U.S.D.A. For. Serv. Misc. Paper PSW-46.
- FORD, E. D. and P. J. NEWBOULD. 1977. The biomass and production of ground vegetation and its relation to tree cover through a deciduous woodland cycle. J. Ecology 65:201–212.
- FRISHKNECHT, N. C. and P. W. CONRAD. 1965. Adaptable, transportable utilization cages. J. Range Managem. 18:33–34.
- GOWANS, K. D. 1958. Soil survey of the Hopland Field Station. California Agricultural Experiment Station, Berkeley, CA.
- GRIFFIN, J. R. 1977. Oak woodland. Pp. 383–415 in M. G. Barbour and J. Major (eds.), Terrestrial vegetation of California. Wiley Interscience, New York.



- HALLS, L. K. and J. L. SHUSTER. 1965. Tree herbage relations in pine-hardwood forests of Texas. *J. Forest.* (Washington) 63:282-283.
- Heady, H. F. and L. RADER. 1958. Modifications on the point frame. *J. Range Managem.* 11:95-96.
- and M. D. PITT. 1979. Reactions of northern California grass-woodland to vegetational conversions. *Hilgardia* 47:51-73.
- HERBERT, F. W. and E. L. BEGG. 1969. Soils of the Yuba area, California. Cooperative Project, Department of Soil and Plant Nutrition, University of California, Davis and County of Yuba, CA.
- HOLLAND, V. L. 1980. Effect of blue oak on rangeland forage production in central California. Pp. 314-318 in T. R. Plumb (tech. coord.), *Ecology, management and utilization of California oaks*. U.S.D.A. Gen. Tech. Report PSW-44.
- JAMESON, D. A. 1967. The relationship of tree overstory and herbaceous understory vegetation. *J. Range Managem.* 20:247-249.
- JANSEN, H. C. 1987. The effect of blue oak removal on herbaceous production on a foothill site in the northern Sierra Nevada. Pp. 343-350 in T. R. Plumb and N. H. Pillsbury (tech. coords.), *Multiple use management of California's hardwood resources*. U.S.D.A. Gen. Tech. Report PSW-100.
- JOHNSON, W., C. M. MCKELL, R. A. EVANS, and L. J. BERRY. 1959. Yield and quality of annual range forage following 2,4-D application on blue oak trees. *J. Range Managem.* 9:18-20.
- KAY, B. L. 1987. Long-term effect of blue oak removal on forage production, forage quality, soil, and oak regeneration. Pp. 351-357 in T. R. Plumb and N. H. Pillsbury (tech. coords.), *Multiple use management of California's hardwood resources*. U.S.D.A. Gen. Tech. Report PSW-100.
- KIMCHANG, K. 1965. Detailed soil survey of San Joaquin Experimental Range, O'Neals, California. In D. A. Duncan (ed.), *Comprehensive network site description—San Joaquin*. U.S. Biol. Program Tech. Rep. No. 296, Natural Resources and Ecology Laboratory, Colorado State University, Fort Collins, CO.
- KNOOP, W. T. and B. H. WALKER. 1985. Interactions of woody and herbaceous vegetation in a southern African savanna. *J. Ecology* 73:235-253.
- LINDSEY, W. C. 1974. Soil survey of the eastern Santa Clara County area, California. U.S. Soil Conservation Service.
- . 1983. Soil survey of San Luis Obispo County, California. Paso Robles area. U.S. Soil Conservation Service.
- McCLARAN, M. P. and J. W. BARTOLOME. 1989. Fire related recruitment in stagnant *Quercus douglasii* populations. *Can. J. For. Res.* (in press).
- McMURTIE, R. and L. WOLF. 1983. A model of competition between trees and grass for radiation, water and nutrients. *Ann. Bot. (London)* 52:449-458.
- MUNZ, P. A. 1968. *A California flora and supplement*. Univ. California Press, Berkeley.
- PARKER, V. T. and C. H. MULLER. 1982. Vegetational and environmental changes beneath isolated live oak trees (*Quercus agrifolia*) in a California annual grassland. *Amer. Midl. Naturalist* 107:69-81.
- PASSOF, P. C., W. J. CLAWSON, and E. L. FITZHUGH. 1985. Preliminary guidelines for managing California's hardwood rangelands. Coop. Ext. Publ. No. 21413, Univ. California.
- PATTEN, D. T. 1978. Productivity and production efficiency of an upper Sonoran desert ephemeral community. *Amer. J. Bot.* 65:891-895.
- PITT, M. D. and H. F. HEADY. 1978. Responses of annual vegetation to temperature and rainfall patterns in northern California. *Ecology* 59:336-350.
- ROGERS, R. S. 1980. Hemlock stands from Wisconsin to Nova Scotia: transition in understory composition along a floristic gradient. *Ecology* 61:178-193.
- SCHOTT, M. R. and R. D. PIEPER. 1985. Influence of canopy characteristics of one-seed juniper on understory grasses. *J. Range Managem.* 38:328-331.



- SORENSEN, T. 1948. A method of establishing groups of equal amplitude in plant sociology based on similarity of species content. *Biol. Skr.* 5:1–34.
- STANGENBERGER, A. G. and J. I. MALLORY. 1981. Index to forest and range soil series in California. Soil-Vegetation Survey, Calif. Dept. Forest. Div. Agric. Sci., Univ. California, Berkeley.
- STEEL, R. G. D. and J. H. TORRIE. 1980. Principles and procedures of statistics: a biometrical approach, 2nd ed. McGraw-Hill, New York.
- TIEDEMAN, A. R. and J. O. KLEMMEDSON. 1977. Effect of mesquite trees on vegetation and soils in the desert grassland. *J. Range Managem.* 3:361–367.
- WALKER, B. H., D. LUDWIG, C. S. HOLLING, and R. M. PETERMAN. 1981. Stability of semi-arid savanna grazing systems. *J. Ecology* 69:473–498.
- YAVITT, J. B. and E. L. SMITH. 1983. Spatial patterns of mesquite associated herbaceous species in an Arizona grassland. *Amer. Midl. Naturalist* 109:89–93.

(Received 25 Apr 1988; revision accepted 8 Apr 1989.)

---

## NOTEWORTHY COLLECTIONS

### BRITISH COLUMBIA

*WOLFFIA COLUMBIANA* Karsten (LEMNACEAE).—Canada, British Columbia, Victoria, water filled ditch N of Blenkinsop Lake with *Spirodella polyrrhiza* (L.) Schleiden, 48°29.2'N, 123°21.6'W, elev. 20 m, 27 Jun 1988, A. & O. Ceska 23775 (V); Victoria, Swan Lake, accumulated along the shore in a stand of *Phalaris arundinacea* L. near the wharf at the Swan Lake Nature Sanctuary, 48°27.9'N, 123°22.2'W, elev. 15 m, 14 Dec 1988, A. Ceska & C. Dorworth 25540 (V).

*Identification.* *Wolffia columbiana* differs from *W. borealis* (Engelm.) Landolt by its globose shape without a flat top, from *W. arrhiza* (L.) Horkel by fewer stomata (up to 10). *Wolffia globosa* (Roxburgh) Den Hertog & van der Plas is smaller than *W. columbiana* and its fronds are slightly elongated. Our identification was confirmed by W. P. Armstrong and E. Landolt.

*Significance.* The first report from British Columbia. In North America *W. columbiana* is frequent in SE USA, and in SE Canada, rare in California [Armstrong, Madroño 31:123–124, 1984; Armstrong and Thorne, Madroño 31:171–179, 1984; Armstrong Fremontia 13(1):11–14, 1985] and Oregon. In western Canada reported from Saskatchewan [as *W. arrhiza*: Looman, Can. Field. Nat. 97:220–222, 1983] and from Alberta [Griffiths, Alberta Naturalist 18(1):18–20, 1988]. For the world distribution data and map see pp. 371–376 in Landolt. The family of Lemnaceae—a monographic study. Veröff. Geobot. Inst. ETH, Stiftung Rübel 71:1–566, 1986.—W. F. SAVALE, JR. and ADOLF CESKA, % Botany Unit, Royal British Columbia Museum, Victoria, BC, V8V 1X4, Canada.



# EFFECTS OF VARYING FIRE REGIMES ON ANNUAL GRASSLANDS IN THE SOUTHERN SIERRA NEVADA OF CALIFORNIA

DAVID J. PARSONS

Research Division, Sequoia and Kings Canyon National Parks,  
Three Rivers, CA 93271

THOMAS J. STOHLGREN

Cooperative National Parks Resources Studies Unit,  
University of California, Davis, CA 95616

## ABSTRACT

Effects of up to three successive spring and fall burns on composition and biomass of the predominantly non-native grasslands of the southern Sierra Nevada foothills were evaluated. Fall and spring burning regimes increased the number and biomass of both alien and native forb species. No native grass species became established following the treatments. Thus, whereas the biomass of alien grass species can be reduced by repeated burning, they will be replaced by increases in both alien and native forbs. Changes seen following one or two burns (spring or fall) were not sustained following cessation of burning treatment.

The annual grasslands that characterize much of California, including the low elevation foothills of the southern Sierra Nevada, are dominated by species native to the Mediterranean Basin (Wester 1981). Prior adaptation to grazing by livestock has favored alien species in the replacement of native grasses and forbs (Barry 1972; Jackson 1985; Macdonald et al. 1988). Analysis of both historical accounts and microfossil remains indicate that areas that once supported either extensive native annual grasslands or *Stipa* bunchgrass prairie are now dominated by alien annual grasses (Barry 1972; Heady 1977; Bartolome et al. 1986). The abilities to withstand drought and grazing have combined to assure the continued dominance of annual Mediterranean grasses. The timing and intensity of precipitation and grazing pressure, including the amount of natural mulch retention, have been shown to significantly influence vegetative production and species composition on annual grassland sites in central California (Talbot et al. 1939; Duncan and Woodmansee 1975; Bartolome et al. 1980). Hervey (1949) quantified the effects of an early summer burn in temporarily favoring broadleaved forbs over grasses on a coastal foothill range and Larson and Duncan (1982) have documented a near doubling of production two years following a fall burn on the San Joaquin Experimental Range near Fresno. Yet, although variable patterns of climate, fire and grazing



result in considerable year to year fluctuation in nonnative annual species composition and biomass (Bentley and Talbot 1958; Heady 1958; Pitt and Heady 1978), those studies showed no indication of successful reestablishment of the native flora.

Land management agencies charged with the preservation of natural ecosystems face the dilemma of either accepting the loss of a significant component of the native flora or attempting to restore a more native species composition. The former, as has been suggested by Heady (1977), requires a compromise in management objectives, essentially declaring alien species as naturalized. The latter requires both a sophisticated knowledge of grassland ecology and a potentially intensive restoration program, if such is even possible. In Sequoia National Park, several thousand hectare of annual grassland are protected as both part of the Park and the Sequoia and Kings Canyon International Biosphere Reserve. National Park Service management policy calls for protection and restoration of this ecosystem. Although effective protection from livestock grazing is provided, the question remains as to whether native species can ever successfully be restored to the area.

An active program of restoring periodic fire to an area where fires have been effectively suppressed for most of a century (Parsons 1981; Bancroft et al. 1985), together with evidence that the frequency and season of fire can influence species composition and production in other grassland communities (Hover and Bragg 1981; Towne and Owensby 1984), led us to test the effects of varying fire regimes on species composition and biomass. Similar experiments, using a combination of seeding, fertilization, and burning, provided mixed results in restoring degraded grasslands in San Diego County (Garcia and Lathrop 1984).

The objectives of this study were to investigate the effects of frequency and season of burning on the relative composition and dominance of native and alien species in the annual grassland communities of the southern Sierra Nevada. Such data are essential to understanding the effects of past and present management practices as well as in evaluating the possibility of using fire as a tool to reestablish native species. This is critical to understanding the short- and long-term impacts of reestablishing natural fire regimes (Parsons et al. 1986).

#### STUDY AREA

The study area is located on a gentle eastern exposure at an elevation of 700 m in the rolling foothills of the drainage of the Middle Fork of the Kaweah River, Sequoia National Park, Tulare County, California. The region is characterized by the hot, dry summers typical of Mediterranean climates (Aschmann 1973). Annual pre-



precipitation, which is concentrated in January, February, and March, averaged 139, 73, 133, and 202 percent, respectively, of the long-term annual average of 68.1 cm during the four study years. Vegetation in the area consists of annual grasslands beneath scattered blue oak (*Quercus douglasii* Hook. & Arn.). Grazing by domestic cattle and horses occurred on the site during the late 1800's and early 1900's but has now been absent for at least 60 years.

The area has no record of burning after a 1960 wildfire burned much of the vicinity (Stocking 1966). Park fire maps record no fires in the area between 1925 and 1960. Prior to the fire protection provided by the creation of Sequoia National Park in 1890, lightning fires, together with intentional ignitions by aboriginals and sheepherders (for a brief period between about 1860 and 1890), are thought to have regularly burned the Sequoia foothills (Vankat and Major 1978; Parsons 1981). Previous studies of vegetation in the area have focused primarily on the overstory oak woodland (Baker et al. 1981; McClaran 1986), and nearby chaparral communities (Stohlgren et al. 1984; Rundel et al. 1987). Soils in the area are characterized by fine to coarse textured sandy loam Ultic Haploxeralfs (Huntington and Akeson 1988). They are derived from granitic bedrock and are moderately deep and moderately well drained.

## METHODS

An area approximately 2.0 ha was selected as representative of the foothill annual grasslands of Sequoia National Park. Seven 10-m by 10-m study sites were identified within this area in positions that maximized chances of successful fire control. The sites were each assigned one of seven fire treatments based on fire logistical concerns. Treatments included a single fall burn (1980; F1), two successive fall burns (1980 and 1981; F2), three successive fall burns (1980, 1981, and 1982; F3), a single spring burn (1980; S1), two successive spring burns (1980 and 1981; S2), three successive spring burns (1980, 1981, and 1982; S3), and an unburned control (C). All fires were carried out as prescribed burns under pre-established prescriptions previously tested to assure both containment and high fuel consumption.

Fall burns were conducted in late October or early November, near the end of the natural fire season (Parsons 1981). During the fall burns fine fuel (cured grass) moisture contents ranged from 10 to 15%, air temperatures from 18 to 21°C, and relative humidities from 40 to 65%. Flame lengths averaged 0.6 to 1.0 m and rate of spread 2.5 to 5.0 m/min. The spring burns were carried out in early to mid-June, after the annual vegetation had dried but before most natural ignitions would normally have occurred (Parsons 1981). Fine fuel moistures ranged from 7 to 9%, air temperatures from 22 to 27°C and relative humidities from 41 to 46%. Flame lengths ranged



from 0.6 to 1.5 m and rate of spread from 4.0 to 20 m/min. All burns resulted in essentially total consumption of vegetative biomass. Burning during the hot dry summer was avoided due to the threat of the fire escaping the area.

Vegetation sampling was carried out annually within five randomly distributed 0.05-m<sup>2</sup> circular plots within each burn treatment (new plots were selected each year). Beginning in the spring of 1980, before the first burn, and continuing through 1983, one growing season following the final burn, all of the current year's vegetative growth was clipped at a height of 1.0 cm above ground level in each plot. Clipped samples were separated by species and oven dried for 24 hours at 94°C to determine dry weight. Sampling was carried out in the spring at peak biomass, before significant seed loss or senescence had occurred. The sampling schedule varied as a function of that year's phenology, falling between 4 May and 24 May. Data collected from the 35 randomly placed 0.05-m<sup>2</sup> plots sampled during the spring of 1980 were used to characterize the pre-study species composition and biomass of the area.

It is recognized that the lack of true replicate treatments may limit interpretation of the data. Due to logistic constraints related to the burn operation the decision was made to focus on multiple treatments at the expense of replication. Possible block effects are minimized by also considering the results as a percent of the 1980 pre-burn condition of the same plots. Statistical analysis of the vegetation data included two-way analysis of variance (ANOVA) to compare the effects of treatment, or burning regime, by year for each of three vegetative groups (alien grasses, alien forbs, and native forbs; no native grasses were encountered) for biomass and species richness. If the F-test ratios were significant ( $p < 0.05$ ) for either factor, Tukey's multiple range test (SAS Institute Inc. 1985) was used to detect significant differences ( $p < 0.05$ ) within the vegetative groups for that factor. We recognize the study design does not fully meet the underlying assumption of an analysis of variance since plots were not randomly assigned treatments (due to fire control logistics constraints). But because of the homogeneity of the pre-burn condition and the severity of the treatments applied, we present the results of the ANOVA as supportive information.

To assess species-specific responses to different burning regimes, percent of total biomass for each major species was calculated following the three successive fall or spring burns and compared to that both preceding treatment (1980) and for the 1983 control.

## RESULTS AND DISCUSSION

The pre-burn 1980 vegetation of the study sites consisted of eighteen species of grasses and forbs with a mean total biomass of 334.5 g/m<sup>2</sup> (Table 1). The 35 sample plots averaged 5.6 species per plot.



TABLE 1. COMPOSITION OF FOOTHILL GRASSLANDS, SEQUOIA NATIONAL PARK. Data based on spring 1980 sampling of 35 randomly placed 0.05-m<sup>2</sup> plots in the seven 100-m<sup>2</sup> study sites. Frequency refers to percentage of the 35 plots in which species occurs.

| Species  | Growth form | Alien/native | Frequency | Biomass g/m <sup>2</sup> ± SE |
|--|-------------|--------------|-----------|-------------------------------|
| <i>Avena fatua</i> L.                              | grass       | A            | 100       | 254.1 ± 18.57                 |
| <i>Bromus mollis</i> L.                            | grass       | A            | 97        | 33.7 ± 5.86                   |
| <i>Bromus diandrus</i> Roth                        | grass       | A            | 83        | 36.3 ± 5.52                   |
| <i>Galium parisiense</i> L.                        | forb        | A            | 46        | 1.0 ± 0.42                    |
| <i>Brodiaea elegans</i> Hoover                     | forb        | N            | 37        | 0.8 ± 0.26                    |
| <i>Bromus sterilis</i> L.                          | grass       | A            | 29        | 1.8 ± 0.71                    |
| <i>Torilis nodosa</i> (L.) Gaertner                | forb        | A            | 26        | 1.6 ± 0.66                    |
| <i>Festuca dertonensis</i> Asch. & Graebner        | grass       | A            | 23        | 2.6 ± 1.33                    |
| <i>Cerastium glomeratum</i> Thuill.                | forb        | A            | 23        | 0.2 ± 0.09                    |
| <i>Madia elegans</i> D. Don                        | forb        | N            | 20        | 0.2 ± 0.14                    |
| <i>Trifolium microcephalum</i> Pursh               | forb        | N            | 20        | 0.8 ± 0.32                    |
| <i>Amsinckia intermedia</i> Fischer & C. Meyer     | forb        | N            | 17        | 0.7 ± 0.35                    |
| <i>Lotus subpinnatus</i> Lagasca                   | forb        | N            | 9         | 0.1 ± 0.08                    |
| <i>Geranium carolinianum</i> L.                    | forb        | N            | 6         | 0.2 ± 0.12                    |
| <i>Festuca megalura</i> Nutt.                      | grass       | A            | 6         | 0.1 ± 0.07                    |
| <i>Plagiobothrys nothofulvus</i> (A. Gray) A. Gray | forb        | N            | 6         | 0.1 ± 0.02                    |
| <i>Euphorbia crenulata</i> Engelm.                 | forb        | N            | 6         | 0.1 ± 0.02                    |
| <i>Lupinus benthamii</i> A. A. Heller              | forb        | N            | 3         | 0.1 ± 0.11                    |



TABLE 2. EFFECT OF TREATMENT BY YEAR ON NUMBER OF SPECIES AND BIOMASS (g/0.05 m<sup>2</sup>) OF ALIEN GRASSES. Only means with different letters within columns (a, b, c) or within rows (i, j, k) are significantly different at  $p < 0.05$ . Treatment codes are C = control, F1 = one fall burn, F2 = two fall burns, F3 = three fall burns, S1 = one spring burn, S2 = two spring burns, S3 = three spring burns.

| Treatment   | Year   |        |        |          |
|-------------|--------|--------|--------|----------|
|             | 1980   | 1981   | 1982   | 1983     |
| No. species |        |        |        |          |
| C           | 3.0    | 3.8    | 3.0    | 3.0 a    |
| F1          | 3.0    | 2.4    | 3.6    | 3.0 a    |
| F2          | 3.8    | 3.2    | 3.2    | 3.6 a    |
| F3          | 3.4    | 3.6    | 3.4    | 2.6 b    |
| S1          | 4.4    | 3.4    | 3.4    | 3.4 a    |
| S2          | 3.8    | 4.4    | 4.4    | 3.8 a    |
| S3          | 3.0    | 3.2    | 3.8    | 4.0 a    |
| Biomass     |        |        |        |          |
| C           | 14.4   | 13.3   | 17.8 i | 10.4 c/j |
| F1          | 15.0   | 17.0   | 11.2   | 9.1      |
| F2          | 20.0 i | 14.1   | 6.7 j  | 12.3 c/j |
| F3          | 19.2 i | 17.3 i | 9.4    | 2.3 a/j  |
| S1          | 13.2   | 14.4   | 18.1   | 17.3 b   |
| S2          | 18.3 i | 11.3   | 8.6 j  | 8.6 j    |
| S3          | 15.0   | 11.9   | 8.6    | 8.1 c    |

*Avena fatua*, a grass introduced from Europe, dominated all plots, constituting 75.0% of the total biomass (range = 63.2 to 89.7%). Three alien grass species, *A. fatua*, *Bromus mollis*, and *B. diandrus*, occurred in nearly every plot and together accounted for 95.5% (range = 90.3 to 99.6) of the total biomass. Broadleaved forbs occurred only sporadically, constituting 5.9 g/m<sup>2</sup> or 1.8% (range = 0 to 10.1%) of the total mean biomass. Alien forbs averaged less than one species and 2.8 g/m<sup>2</sup> whereas native forbs averaged 1.3 species and 3.1 g/m<sup>2</sup>. Non-native species dominated all plots in both frequency and biomass. Although a total of nine native species were encountered, only *Brodiaea elegans* was found in more than 20% of the plots, and all nine together accounted for less than one percent of the total biomass (Table 1). This pre-treatment composition is similar to that found in other ungrazed or lightly grazed California annual grassland sites (Heady 1977).

The only detected pre-burn significant differences between plots located in the different treatment areas were for number of species and biomass of alien forbs in the site to receive a single spring burn (S1) and biomass of native forbs in the site to receive two successive spring burns (S2). The only significant differences found between years for the control plot were for biomass of alien grasses (1982–1983), and number of species of alien forbs (1980–1981) (see Tables



TABLE 3. EFFECT OF TREATMENT BY YEAR ON NUMBER OF SPECIES AND BIOMASS (g/0.05 m<sup>2</sup>) OF ALIEN FORBS. Only means with different letters within columns (a, b, c) or within rows (i, j, k) are significantly different at  $p < 0.05$ . Treatment codes are C = control, F1 = one fall burn, F2 = two fall burns, F3 = three fall burns, S1 = one spring burn, S2 = two spring burns, S3 = three spring burns.

| Treatment   | Year     |         |         |         |
|-------------|----------|---------|---------|---------|
|             | 1980     | 1981    | 1982    | 1983    |
| No. species |          |         |         |         |
| C           | 0.4 a/i  | 2.4 a/j | 1.2 a   | 1.2 a   |
| F1          | 0.6 a/i  | 2.4 a/j | 3.6 b/j | 2.4 j   |
| F2          | 1.0 i    | 5.4 b/j | 4.2 b/j | 3.6 b/k |
| F3          | 0.8 a/i  | 3.2 j   | 3.8 b/j | 4.0 b/j |
| S1          | 2.6 b    | 3.6     | 3.8 b   | 2.8     |
| S2          | 0.6 a/i  | 2.6 a/j | 3.4 b/j | 3.2 j   |
| S3          | 0.8 a/i  | 3.6 j   | 4.0 b/j | 4.0 b/j |
| Biomass     |          |         |         |         |
| C           | 0.1 a    | 0.3 a   | 0.8 a   | 0.8 a   |
| F1          | 0.01 a/j | 1.9 j   | 7.6 b/i | 1.9 j   |
| F2          | 0.1 a/j  | 2.9 j   | 7.3 b/i | 2.7 b/j |
| F3          | 0.03 a/i | 4.2 b/j | 3.6 j   | 5.4 b/j |
| S1          | 0.7 b    | 1.5     | 2.8     | 1.2     |
| S2          | 0.03 a/i | 0.7 i   | 1.7 a/j | 3.2 b/k |
| S3          | 0.1 a/i  | 2.1 i   | 8.1 b/j | 4.3 b/j |

2–4). This shows strong similarity between the pre-burn character of the seven treatment areas as well as a consistent year to year character for the unburned control.

Two-way ANOVA of treatment and year for each vegetation group detected significant effects ( $p < 0.05$ ) of both treatment and year on all but the number of alien grass species. Treatment effects influenced the biomass of the different vegetation groups as well as the number of native and alien forb species.

Together, the burn treatments resulted in the appearance of 18 additional native forb species, five additional alien forb species, and no new grass species. The most important of these species are discussed in the text.

Figures 1 and 2 summarize the effects of one, two, and three successive fall and spring burns on the relative biomass of alien grasses, alien forbs and native forbs. Under both burning regimes the biomass of alien grasses is decreased relative to that of both alien and native forbs. Tables 2–4 detail the effects of the six experimental burning regimes on number of species and biomass of these three vegetative groups.

Alien grasses appear to be minimally affected by the fall burning regimes. Species richness (and composition) is not influenced by successive fall burns (Table 2). Whereas biomass of alien grasses is



TABLE 4. EFFECT OF TREATMENT BY YEAR ON NUMBER OF SPECIES AND BIOMASS (g/0.05 m<sup>2</sup>) OF NATIVE FORBS. Only means with different letters within columns (a, b, c) or within rows (i, j, k) are significantly different at p < 0.05. Treatment codes are C = control, F1 = one fall burn, F2 = two fall burns, F3 = three fall burns, S1 = one spring burn, S2 = two spring burns, S3 = three spring burns.

| Treatment   | Year     |          |         |         |
|-------------|----------|----------|---------|---------|
|             | 1980     | 1981     | 1982    | 1983    |
| No. species |          |          |         |         |
| C           | 0.6      | 1.2 a    | 0.8 a   | 1.6 a   |
| F1          | 1.0      | 3.0      | 2.2     | 1.0 a   |
| F2          | 2.0      | 3.0      | 3.4     | 3.6 b   |
| F3          | 0.4 i    | 3.0 j    | 1.8     | 4.2 b/j |
| S1          | 1.4      | 3.6 b    | 3.2     | 1.6 a   |
| S2          | 2.6 i    | 5.8 b/j  | 4.4 b/j | 2.2 i   |
| S3          | 1.0 i    | 4.4 b/j  | 3.2 j   | 3.2 j   |
| Biomass     |          |          |         |         |
| C           | 0.1 a    | 0.7 a    | 0.37    | 0.5 a   |
| F1          | 0.01 a/i | 6.4 j    | 0.8 i   | 0.4 a/i |
| F2          | 0.2 a    | 3.1      | 6.2     | 2.5     |
| F3          | 0.02 a/i | 6.2 j    | 1.5     | 2.1     |
| S1          | 0.6 a/i  | 12.4 b/j | 2.1 i   | 0.9 i   |
| S2          | 0.6 b/i  | 5.9 j    | 3.3     | 0.8 i   |
| S3          | 0.1 a/i  | 5.3 j    | 2.9     | 3.5 b   |

decreased over pre-treatment levels by two fall burns, it is only after three such burns that biomass (11% of pre-burn) also differs from numbers found in the control plots. Decreases in abundance of *Avena fatua* and *Bromus diandrus* account for most of the biomass change.

Both the number of species and biomass of alien forbs increased over pre-burn and control levels following two or more fall burns (Table 3). Alien forb biomass increased as much as 12,000% following two fall burns (F2; 1982) and 18,000% following three fall burns (F3; 1983) over pre-burn levels in the same plots. Although an increased number of species is still evident following a year of recovery in the F2 plot, biomass has dropped markedly (Table 3). A single species, *Centaurea melitensis* L., which was not encountered in any plots during pre-burn sampling and only rarely found in the control plots in succeeding years, accounts for the majority of the alien forb response. Other alien forb species that increased with fall burning include *Silene gallica* L., *Galium parisiense*, and *Hypochaeris glabra* L.

Whereas native forbs increased in both species richness and biomass following fall burning, only the number of species following three successive fall burns (F3) differed from both pre-burn and control levels (Table 4). Native forb biomass increased sharply fol-



lowing an initial burn and maintained moderately high levels in the following years. *Lotus subpinnatus* and *Orthocarpus attenuatus* A. Gray were the native forb species exhibiting the largest and most consistent increases following fall burning. Although up to three successive fall burns clearly influenced relative species composition and dominance, including increasing the relative importance of both native and alien forbs at the expense of alien grasses (Fig. 1) it is uncertain what fire return interval would be required to maintain such changes or whether they would revert to pre-burn levels following a short time without fire. By the end of the study in 1983, it is only in the plot burned for three successive years (F3) that alien grasses do not dominate total biomass. Increases in the forb groups following one or two burns in the other fall treatments either have returned or have begun to approach pre-burn levels. Additional time would be required to determine if the relative suppression of alien grasses achieved with three fall burns could be maintained.

Whereas total biomass tended to increase following an initial fall burn, it returned to near control levels in succeeding years. The minimal influence of repeated fall burning on total productivity counters other findings that the amount of mulch residue strongly influences productivity in California's annual grasslands (Bartolome et al. 1980).

Spring burning, although probably not as important a part of historical southern Sierra Nevada foothill fire regimes as summer and fall burns, does show some potential for altering composition of annual grasslands. Total species richness was increased by successive spring burns, a difference due entirely to increased numbers of forbs. Total biomass was not influenced by spring burning (Tables 2–4). Spring burning showed little effect on alien grasses, other than a substantial but not statistically significant decrease in biomass (Table 2, Fig. 2).

Species richness and biomass of alien forbs increased following two or three spring burns. Biomass (Fig. 2) increased by as much as 135-fold (from 0.1 to 8.1 g/0.05 m<sup>2</sup>) in the 1982 F3 plot (Table 3). Alien forb species, including *Silene gallica* L., *Erodium botrys* (Cav.) Bertol., and *Hypochoeris glabra* L., increased significantly following spring burns.

An initial spring burn dramatically increased both the number of species and biomass of native forbs. However, these increases either returned to near pre-burn levels with the cessation of fire (S1 and S2) or stabilized at slightly lower levels even with repeated annual burning (F3; Table 4). *Trifolium microcephalum*, *Lupinus benthamii*, and *Lotus subpinnatus* are the major native forbs that increased following spring burning. Increases in *L. benthamii* were not sustained following the initial burn.

Table 5 lists those species that were influenced most by three



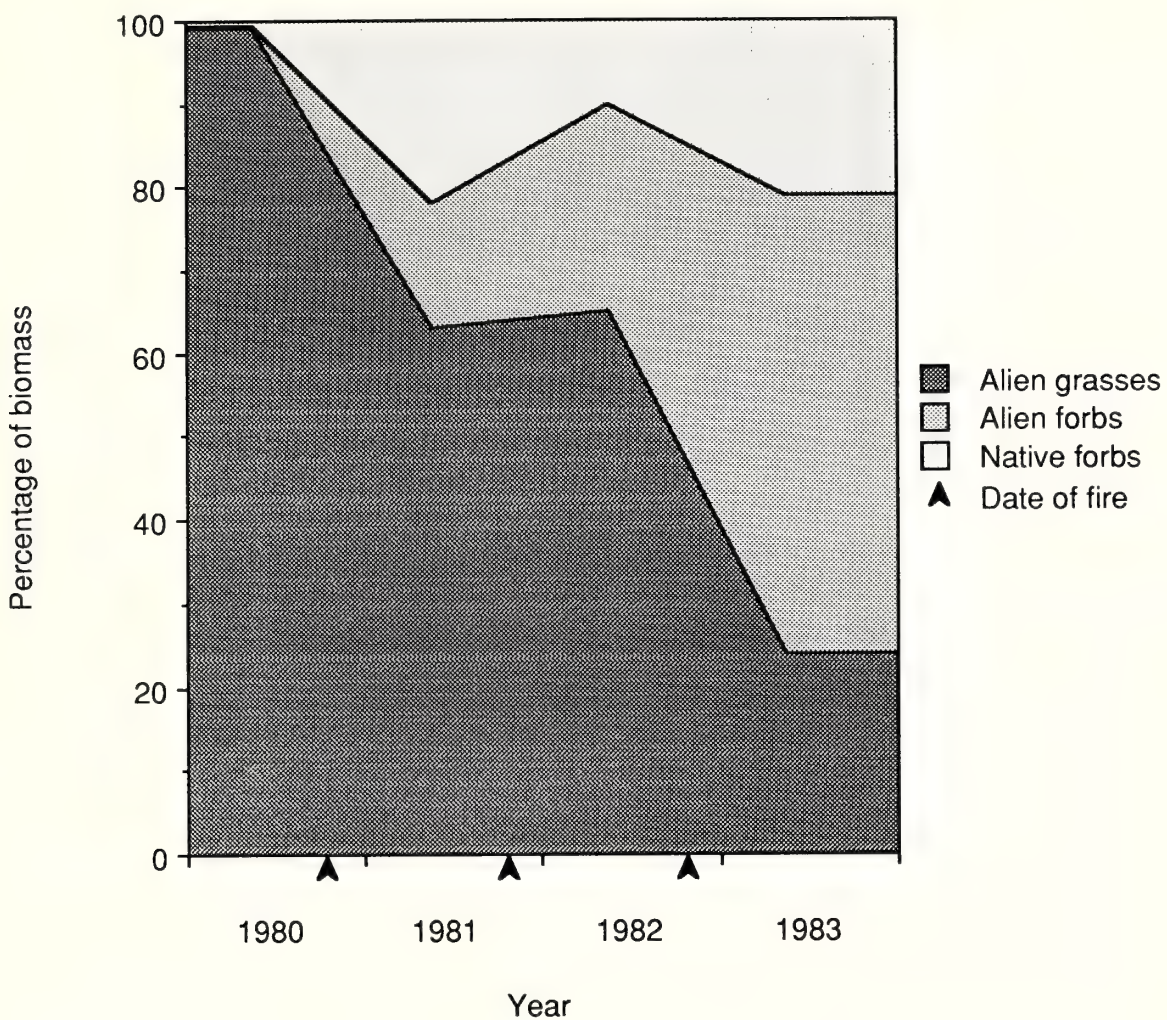


FIG. 1. Percentage of total plot biomass for alien grasses, alien forbs, and native forbs following 1, 2, and 3 successive fall burns. Data from 5 0.05-m<sup>2</sup> plots located in F3 (three fall burns) treatment.

successive fall or spring burns. Burning in either season resulted in dramatic reductions in dominance of the omnipresent *Avena fatua*. This invasive European grass dominates much of the annual grasslands throughout California. Three successive fall burns reduced *A. fatua* to 5.3% of the total biomass whereas three successive spring burns reduced it to 12.4% (Table 5). A second common introduced grass, *Bromus diandrus*, was also reduced to minimal presence (0.2 and 1.3%, respectively) by successive fall or spring burns. The third dominant grass of the unburned grassland, *Bromus mollis*, was not significantly affected by burning in either season, contributing between 10 and 27% of the total biomass of both pre- and post-burn plots.

Both the F3 and S3 treatments shifted the relative dominance of both species number and biomass from grasses to forbs. Successive fall burns resulted in a dramatic increase of the alien forb *Centaurea melitensis* from non-existent in 1980 to 46.3% of the total biomass in 1983. Alien and native forbs together accounted for 8.2 of the



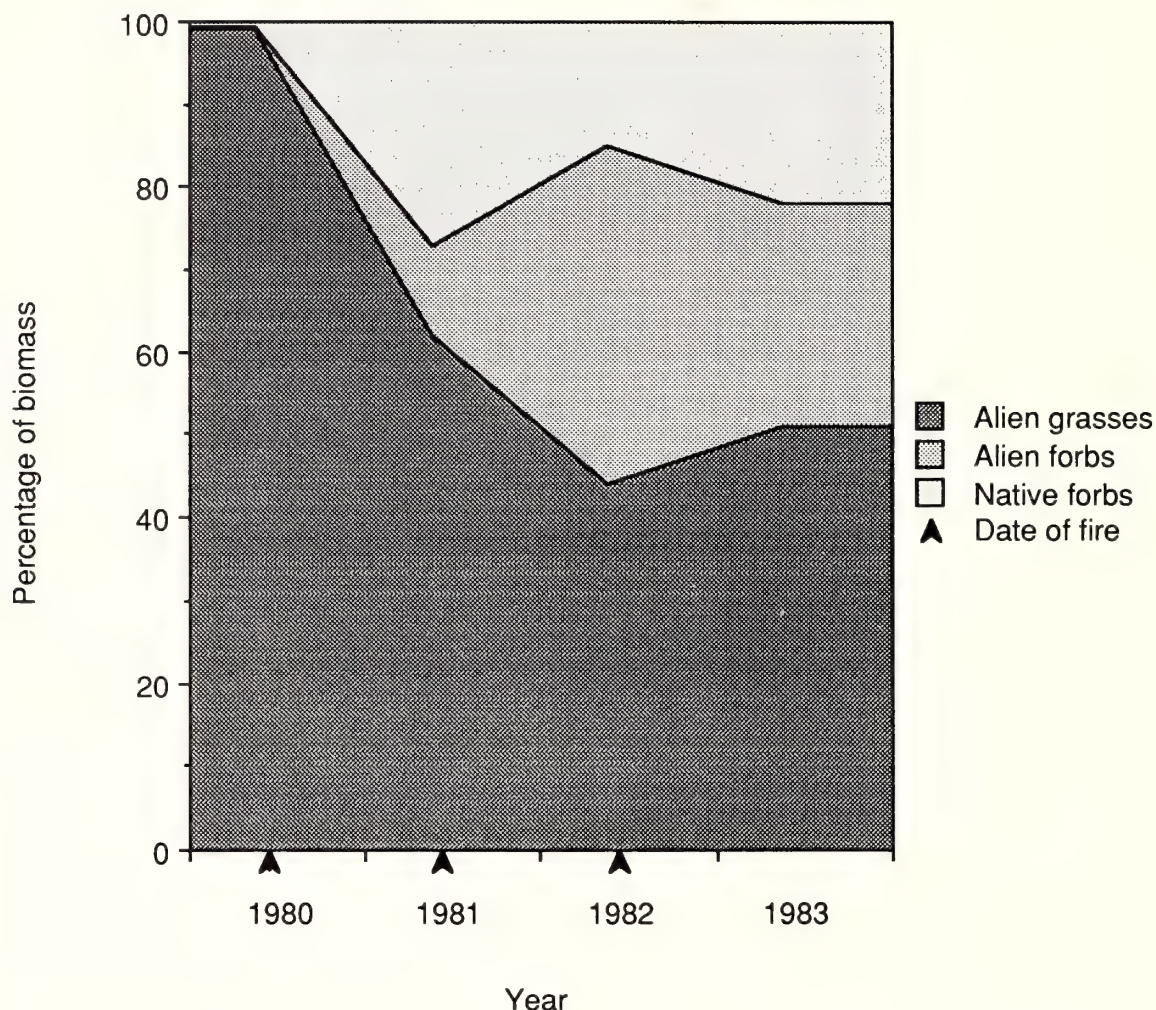


FIG. 2. Percentage of total plot biomass for alien grasses, alien forbs, and native forbs following 1, 2, and 3 successive spring burns. Data from 5 0.05-m<sup>2</sup> plots located in S3 (three spring burns) treatment.

average 10.8 (76%) species per plot (as compared to 1.2 of the 4.6 or 26% in the same plots before burning and 2.8 of 5.8 or 48% of the 1983 control plots) and 7.5 of the average 9.8 g/0.05 m<sup>2</sup> (76%) (as compared to 0.05 of 19.2 g/0.05 m<sup>2</sup> or 0.2% before burning and 1.3 of 11.7 or 11% of the control plots). Five species of forbs (3 alien and 2 native) accounted for 71.6% of the total post-treatment biomass. The same five species were completely absent from these plots in 1980 and together accounted for only 0.3% of the total biomass in the 1983 control plots (Table 5). A total of six native and six alien forb species were encountered following the three fall burns.

While three successive spring burns also increased the relative importance of forbs over grasses, the magnitude of the shift was less and the species composition different from that observed following fall burning. The five most common forbs following three successive spring burns included two native and three alien species. Together these contributed 43.6% of the total biomass (Table 5). A total of



TABLE 5. SPECIES SHOWING MAJOR CHANGE IN RELATIVE BIOMASS FOLLOWING THREE SUCCESSIVE FALL (F3; 1983) AND/OR THREE SUCCESSIVE SPRING (S3; 1983) BURNS AS COMPARED WITH PREBURN (1980) AND CONTROL (C; 1983) PLOTS. Data presented as percentage of total plot biomass. Growth form codes are A = alien, N = native, F = forb, G = grass.

| Species                        | Growth form | Control (1983) | Preburn (1980) | Postburn (1983) |
|--------------------------------|-------------|----------------|----------------|-----------------|
| Fall burn increasers           |             |                |                |                 |
| <i>Centaurea melitensis</i>    | AF          | 0.1            | 0.0            | 46.3            |
| <i>Lotus subpinnatus</i>       | NF          | 0.0            | 0.0            | 10.8            |
| <i>Silene gallica</i>          | AF          | 0.1            | 0.0            | 5.3             |
| <i>Hypochoeris glabra</i>      | AF          | 0.1            | 0.0            | 4.8             |
| <i>Orthocarpus attenuatus</i>  | NF          | 0.0            | 0.0            | 4.4             |
| Fall burn decreaseers          |             |                |                |                 |
| <i>Avena fatua</i>             | AG          | 39.0           | 89.7           | 5.3             |
| <i>Bromus diandrus</i>         | AG          | 12.0           | 10.8           | 0.2             |
| Spring burn increasers         |             |                |                |                 |
| <i>Erodium botrys</i>          | AF          | 0.0            | 0.0            | 15.8            |
| <i>Trifolium microcephalum</i> | NF          | 0.1            | 0.5            | 11.0            |
| <i>Silene gallica</i>          | AF          | 0.1            | 0.0            | 7.5             |
| <i>Lotus subpinnatus</i>       | NF          | 0.0            | 0.0            | 6.9             |
| <i>Festuca megalura</i>        | AG          | 0.0            | 0.1            | 6.2             |
| <i>Centaurea melitensis</i>    | AF          | 0.1            | 0.0            | 2.4             |
| Spring burn decreaseers        |             |                |                |                 |
| <i>Avena fatua</i>             | AG          | 39.0           | 76.5           | 12.4            |
| <i>Bromus diandrus</i>         | AG          | 12.0           | 12.9           | 1.3             |

five native and six alien forb species were encountered. The most common post-burn species following three successive spring fires were *Erodium botrys*, an alien introduced from Europe, and the native *Trifolium microcephalum*. Neither of these increased substantially following fall burns (Table 5). Alien and native forbs together accounted for 7.2 of the 11.2 species per plot (64%) (as opposed to 1.8 of 4.8 or 38% before burning and 2.8 of 5.8 or 48% of the control plots) and 7.8 of the 15.9 g/0.05 m<sup>2</sup> (49%) (compared with 0.2 of 15.2 g/0.05 m<sup>2</sup> or 1.3% preburn and 1.3 of 11.7 or 11% of the control plots) biomass.

### CONCLUSIONS

The annual grasslands that characterize much of the foothills of the southern Sierra Nevada are dominated by species introduced from Europe and other Mediterranean climate areas. The near complete dominance of these species has been largely attributed to their resistance to disturbance associated with grazing, erosion and agriculture. The role of fire in the competitive interaction between native



and alien species in California's grasslands is uncertain. In natural areas such as national parks and nature preserves there is interest in reestablishing the native herbaceous flora. The experiments reported here indicate that both the frequency and seasonality of fire can influence grassland species composition and biomass. Both spring and fall burning increased the total number of species. Repeated burns both decreased the relative dominance of introduced grasses and increased the diversity and dominance of native and alien forbs. Neither single nor repeated (up to three times) fall or spring burns resulted in the establishment of additional species of native grasses in the study area. This may, in part, be attributed to the fact that native grass species and thus seed sources are rare in this community.

Although both fall and spring burns favored forb establishment at the expense of grasses, they had minimal effect on total biomass when maintained over three years. Fall burns tended to increase the number and biomass of alien forbs more than that of native species whereas spring burns favored both about equally. Thus, although the number and biomass of alien grasses may be reduced by regular and repeated burning (especially late in the season), both alien and native forbs will be increased.

In the case of both fall and spring burning, alien grasses quickly regained their pretreatment dominance when burning was halted following one or two treatments. From a management perspective, this means that whatever gains might be realized from a program of regular burning could be quickly lost if that program were suspended. Frequent burning will almost certainly be needed to maintain long-term changes if such is even possible.

#### ACKNOWLEDGMENTS

We thank Steve DeBenedetti and Nate Stephenson for assisting with field work and preliminary data summaries. Sylvia Haultain-Tweed provided final data summaries. Mitch McClaran, Ray Ratliff, Steve DeBenedetti, James Bartolome, and Jon Keeley critically reviewed an earlier version of the manuscript. Neil Willits provided statistical consultation.

#### LITERATURE CITED

- ASCHMANN, H. 1973. Distribution and peculiarity of Mediterranean ecosystems. Pp. 11–20 in F. di Castri and H. A. Mooney (eds.), *Mediterranean type ecosystems—origin and structure*. Springer-Verlag, New York.
- BAKER, G. A., P. W. RUNDEL, and D. J. PARSONS. 1981. Ecological relationships of *Quercus douglasii* (Fagaceae) in the foothill zone of Sequoia National Park, California. *Madroño* 28:1–12.
- BANCROFT, L., T. NICHOLS, D. PARSONS, D. GRABER, B. EVISON, and J. VAN WAGTENDONK. 1985. Evolution of the natural fire management program at Sequoia and Kings Canyon National Parks. Pp. 174–180 in *Proceedings, Wilderness Fire Symposium*. U.S.D.A. Forest Service Gen. Tech. Report INT-182.



- BARRY, W. J. 1972. California prairie ecosystems (Vol. I): the Central Valley prairie. California Department of Parks and Recreation, Sacramento. 81 pp.
- BARTOLOME, J. W., S. E. KLUKKERT, and W. J. BARRY. 1986. Opal phytoliths as evidence for displacement of native Californian grassland. *Madroño* 33:217–222.
- , M. C. STROUD, and H. F. HEADY. 1980. Influence of natural mulch on forage production on differing California annual range sites. *J. Range Managem.* 33:4–8.
- BENTLEY, J. R. and M. W. TALBOT. 1948. Annual plant vegetation of California foothills as related to range management. *Ecology* 29:72–79.
- DUNCAN, D. A. and R. G. WOODMANSEE. 1975. Forecasting forage yield from precipitation in California's annual rangeland. *J. Range. Managem.* 28:327–329.
- GARCIA, D. and E. W. LATHROP. 1984. Ecological studies on the vegetation of an upland grassland (*Stipa pulchra*) range site in Cuyamaca Rancho State Park, San Diego County, California. *Crossosoma* 9(7):5–12.
- HEADY, H. F. 1958. Vegetational changes in the California annual type. *Ecology* 39:402–416.
- . 1977. Valley grassland. Pp. 491–533 in M. G. Barbour and J. Major (eds.), *Terrestrial vegetation of California*. John Wiley and Sons, New York.
- HERVEY, D. F. 1949. Reaction of a California annual-plant community to fire. *J. Range Managem.* 2:11–121.
- HOVER, E. I. and T. B. BRAGG. 1981. Effect of season of burning and mowing on an eastern *Stipa*-*Andropogon* prairie. *Amer. Midl. Naturalist* 105:13–18.
- HUNTINGTON, G. L. and M. A. AKESON. 1988. Soil resource inventory of Sequoia National Park, central part, California. Dept. Land, Air and Water Resources, Univ. California, Davis.
- JACKSON, L. E. 1985. Ecological origins of California's Mediterranean grasses. *J. Biogeogr.* 12:349–361.
- LARSON, J. R. and D. A. DUNCAN. 1982. Annual grassland response to fire retardant and wildfire. *J. Range Managem.* 35:700–703.
- MACDONALD, I. A. W., D. M. GRABER, S. DEBENEDETTI, R. H. GROVES, and E. R. FUENTES. 1988. Introduced species in nature reserves in Mediterranean-type climate regions of the world. *Biol. Conserv.* 44:37–66.
- MCCLARAN, M. P. 1986. Age structure of *Quercus douglasii* in relation to livestock grazing and fire. Ph.D. dissertation. Univ. California, Berkeley. 119 pp.
- PARSONS, D. J. 1981. The historical role of fire in the foothill communities of Sequoia National Park. *Madroño* 28:112–120.
- , D. M. GRABER, J. K. AGEE, and J. W. VAN WAGTENDONK. 1986. Natural fire management in national parks. *Environ. Managem.* 10:21–24.
- PITT, M. D. and H. F. HEADY. 1978. Responses of annual vegetation to temperature and rainfall patterns in northern California. *Ecology* 59:336–350.
- RUNDEL, P. W., G. A. BAKER, D. J. PARSONS, and T. J. STOHLGREN. 1987. Postfire demography of resprouting and seedling establishment by *Adenostoma fasciculatum* in the California chaparral. Pp. 575–591 in J. D. Tenhunen, F. M. Catarino, O. L. Lange, and W. C. Oechel (eds.), *Plant response to stress, functional analysis in Mediterranean ecosystems*. Springer-Verlag, New York.
- SAS INSTITUTE, INC. 1985. SAS/STAT guide for personal computers, version 6. Cary, NC.
- STOCKING, S. 1966. Influences of fire and sodium-calcium borate on chaparral vegetation. *Madroño* 18:193–203.
- STOHLGREN, T. J., D. J. PARSONS, and P. W. RUNDEL. 1984. Population structure of *Adenostoma fasciculatum* in mature stands of chamise chaparral in the southern Sierra Nevada, California. *Oecologia* 64:87–91.
- TALBOT, M. W., H. H. BISWELL, and A. L. HORMAY. 1939. Fluctuations in the annual vegetation of California. *Ecology* 20:394–402.



- TOWNE, G. and C. OWENSBY. 1984. Long-term effects of annual burning at different dates in ungrazed Kansas tallgrass prairie. *J. Range Managem.* 37:392–397.
- VANKAT, J. L. and J. MAJOR. 1978. Vegetation changes in Sequoia National Park, California. *J. Biogeogr.* 5:377–402.
- WESTER, L. 1981. Composition of native grasslands in the San Joaquin Valley, California. *Madroño* 28:231–241.

(Received 16 Dec 1988; revision accepted 11 May 1989.)

## CALIFORNIA BOTANICAL SOCIETY

### MEETING PROGRAM 1989–1990

#### “PLANT CONSERVATION RESEARCH NEEDS FOR THE 1990’S”

8:00 P.M. University of California, Berkeley 159 Mulford Hall

| <u>DATE</u> | <u>SPEAKER AND TOPIC</u>   |
|-------------|--|
| 19 OCT      | MR. NIAL McCARTEN, Dept. of Integrative Biology, Univ. California, Berkeley<br>“Plant extinction rates in the California flora: outlook for the future”                    |
| 16 NOV      | MR. TIMOTHY KRANTZ, Botanical Consultant, Haward, CA<br>“Rare and endemic plants of the Big Bear Preserve, San Bernardino County”  |
| 18 JAN      | MR. JAMES BARTEL, U.S. Fish and Wildlife Service, Sacramento, CA<br>“Rarity or endangerment: a call for a consensus on priorities”   |
| 17 FEB*     | DR. MICHAEL SOULE, Dept. of Environmental Studies, Univ. California, Santa Cruz<br>“A zoologist’s perspective on plant conservation biology”                               |
| 15 MAR      | DR. THOMAS GRIGGS, The Nature Conservancy<br>“Restoration of Riparian Systems”   |
| 19 APR      | DR. BRUCE PAVLIK, Dept. of Biology, Mills College, Oakland, CA<br>“Genetic and ecological aspects of rare plant reintroduction: the case of <i>Amsinckia grandiflora</i> ” |
| 17 MAY**    | MS. ROXANNE BITTMAN, Natural Diversity Data Base, Calif. Dept. of Fish and Game, Sacramento<br>“Plant conservation research needs for the 1990’s”                          |

\* **Annual Banquet**—location to be announced.

\*\* Meeting to be held at University of California Botanical Garden, Strawberry Canyon, Berkeley.



# PHYTOGEOGRAPHICAL NOTES ON ACIDOPHILOUS *CLADONIA* SPECIES IN CALIFORNIA

SAMUEL HAMMER<sup>1</sup>

San Francisco State University, San Francisco, CA 94132

## ABSTRACT

Several species in the lichen genus *Cladonia* (Ascomycotina: Lecanorales) and their restricted ranges in California are discussed. *Cladonia carneola*, *C. phyllophora*, *C. cervicornis* subsp. *cervicornis*, and *C. crispata* s. str. grow in small populations on azonally occurring, extremely acidic soils (pH 2.9–4.0) in Mendocino and Amador counties. The taxa at these localities are reproductively isolated from other *Cladonia* populations. Isolation is more marked at the Amador County sites, where only one subsection of the genus is represented. *Cladonia cervicornis* specimens from acidic substrata in Amador County contain the *p*-depside atranorin, an unusual and primitive chemical constituent for this species. In contrast to vascular plant species, which are represented by restricted endemic taxa at these sites, the *Cladonia* populations discussed in this paper belong to cosmopolitan taxa whose ranges are very restricted in California. These taxa are represented by relictual populations at the sites studied.

Of 32 *Cladonia* taxa in California (Hammer 1988) four taxa show distinct distributional patterns on acidic soils. Two areas in northern California are noteworthy for their azonal, conspicuously acidic soil types. Several sites in Mendocino County are characterized by shallow lateritic soils underlain by a hardpan layer that is impenetrable to plant roots. These soils and the pygmy forest that grows on them have been discussed by a number of authors (Jenny et al. 1969; Kruckeberg 1969). Unique patterns of endemism in vascular plants of the pygmy forest were noted by Mason (1946a, b) and McMillan (1956). Jenny et al. briefly mentioned the lichens of the pygmy forest and Malachowski (1975) treated the macrolichen flora of the area.

The Ione Formation, which is composed of outcroppings of a unique exhumed oxisol, lies in the foothills of the Sierra Nevada in Amador County. It shares the acidic properties and underlying hardpan of the pygmy forest. Its geological history and soil characteristics were discussed in Singer and Nkedi-Kizza (1980). Gankin and Major (1964) and Stebbins and Major (1965) discussed the flora of the Ione Formation, focusing on the endemic plant *Arctostaphylos myrtifolia* C. Parry that grows in extremely restricted populations on Ione Formation outcroppings. *Arctostaphylos myrtifolia* is taxonomically closely related to *A. nummularia* A. Gray, which is endemic to the

<sup>1</sup> Present address: The Farlow Herbarium, Harvard University Herbaria, 20 Divinity Avenue, Cambridge, MA 02138.



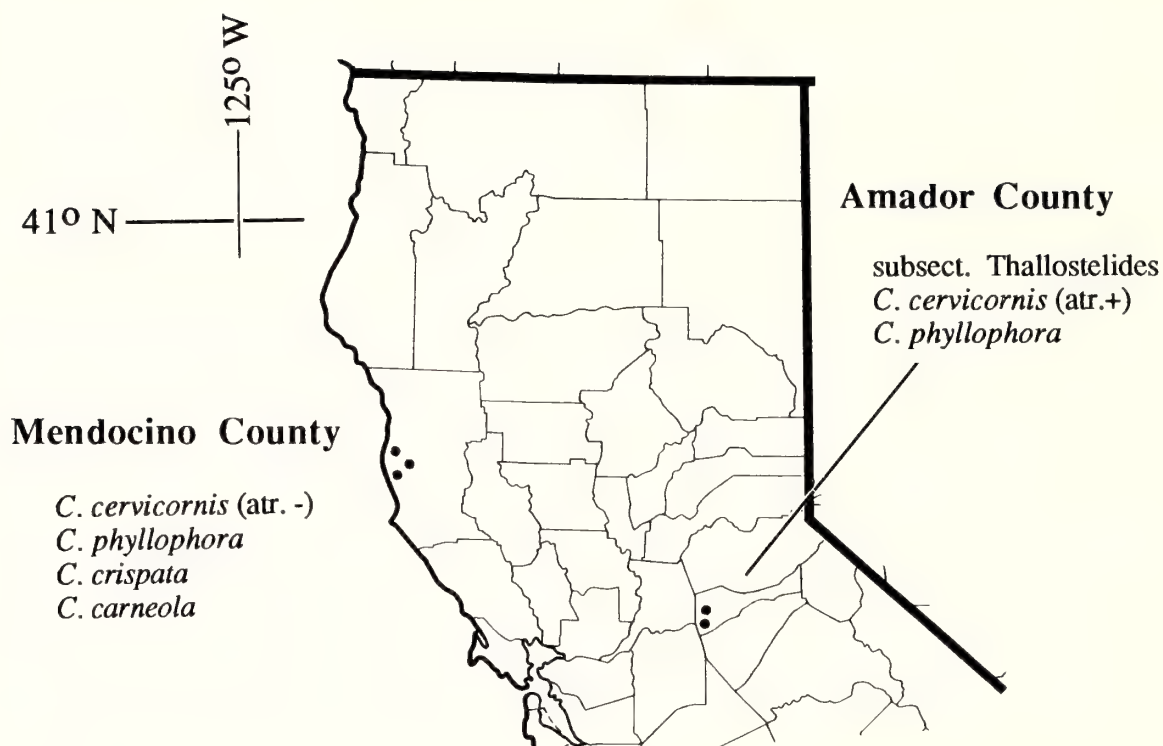


FIG. 1. Acidophilous *Cladonia* taxa found in Pygmy Forest (Mendocino County) and Ione Formation (Amador County) sites.

pygmy forest. These narrowly restricted species are both endemic to conspicuously acidic soils in California. The lichen flora of the Ione Formation was mentioned in Gankin and Major but not treated in detail.

#### MATERIALS AND METHODS

Over 3000 collections of *Cladonia* from California were studied from fresh collections and herbarium specimens over a 2-year period. Several hundred collections of *Cladonia* were studied from five sites in the pygmy forest and the Ione Formation. The pygmy forest sites in Mendocino County lie in or adjacent to Jackson State Forest, approximately 39°15'N, within 3 km of the Pacific coast. The two collecting sites in Amador County are approximately 30 km east of Sacramento, at approximately 38°30'N, in the western foothills of the Sierra Nevada (Fig. 1). Collection citations from both sites are in Hammer (1988).

Preliminary examination of specimens was performed using a dissecting microscope and routine chemical spot tests (White and James 1985). *Cladonia phyllophora* Hoffm., *C. crispata* (Achar.) Flotow, and *C. carneola* (Fries) Fries were positively determined in this way. Several thalli of *C. cervicornis* (Achar.) Flotow subsp. *cervicornis* exhibited an equivocal reaction to the application of potassium hydroxide and were subsequently tested for chemical constit-



uents using thin layer chromatography (TLC). Specimens that performed unequivocally in the spot test (i.e., only fumarprotocetraric acid detected), were not subjected to TLC. Solvent systems "A" and "C" were used (Culberson 1974; Culberson et al. 1981; White and James 1985). Thirty-one thalli of *C. cervicornis* were tested by TLC to detect atranorin. Purified atranorin from a chemical supply company was used as a standard.

## RESULTS

All four taxa discussed in this paper were collected at the pygmy forest sites. All of these taxa were rare in the pygmy forest, growing on bare soil or under *Arctostaphylos* shrubs. Only *C. cervicornis* was represented by more than 10 collections at the pygmy forest localities. The Ione Formation yielded only specimens of *C. phyllophora* and *C. cervicornis*. These species were observed as the dominant terricolous lichens at the Ione Formation sites, where they were found growing in abundance under *A. myrtifolia*.

Atranorin was detected in 16 of the 31 specimens of *C. cervicornis* subsp. *cervicornis* that were tested by TLC. This substance was found in addition to the depsidone fumarprotocetraric acid, which is typically present in *C. cervicornis*. Atranorin was detected in most (80%) of the Amador County specimens, but was rare in specimens from Mendocino County (>10%), where it was present in only trace amounts.

## DISCUSSION

The four taxa of *Cladonia* examined in this paper demonstrate distinct distributional patterns in relation to their isolation on acidic substrata. *Cladonia carneola* is found at one locality outside of the pygmy forest in the Klamath Region of northwestern California. Here it comprises part of a relictual flora that is at least as old as the Pleistocene (Hammer 1989) and may be of Tertiary origins (Raven and Axelrod 1978). *Cladonia crispata* s. str. is restricted to two sites in the pygmy forest, and is not found elsewhere in the state. *Cladonia phyllophora*, rare in the pygmy forest and the Klamath Region of northwestern California, is co-dominant with *C. cervicornis* subsp. *cervicornis* at the Ione Formation sites. *Cladonia cervicornis* s. lat. is distributed widely in California, and subsp. *cervicornis*, of which a few coastal specimens contained atranorin, is present along the Pacific coast from San Diego County to Del Norte County (Fig. 1).

Analysis of the chemical data on *C. cervicornis* from the Ione Formation sites supports the hypothesis that these specimens represent an ancestral population. This population has experienced long geographical and reproductive isolation from other populations in



TABLE 1. *CLADONIA* TAXA PRESENT AT PYGMY FOREST AND IONE FORMATION SITES. Asterisks indicate acidophilous taxa discussed in this paper.

| Pygmy forest (Mendocino County)  | Ione formation (Amador County) |
|--|--------------------------------|
| Sect. <i>Cladonia</i>  |                                |
| Subsect. <i>Cocciferae</i> (Del. in Duby) Mattick                                    |                                |
| <i>C. polydactyla</i> (Flörke) Sprengel s. lat.                                      |                                |
| <i>C. transcendens</i> (Vainio) Vainio   |                                |
| <i>C. macilenta</i> Hoffm.   |                                |
| <i>C. bellidiflora</i> (Achar.) Schaer.  |                                |
| Subsect. <i>Ochroleucae</i> (Fries) Mattick  |                                |
| * <i>C. carneola</i> (Fries) Fries   |                                |
| Subsect. <i>Thallostelides</i> (Vainio) Mattick                                      |                                |
| * <i>C. phyllophora</i> Hoffm.   |                                |
| * <i>C. cervicornis</i> (Achar.) Flotow subsp. <i>cervicornis</i>                    |                                |
| <i>C. cervicornis</i> subsp. <i>verticillata</i> (Hoffm.) Ahti                       |                                |
| <i>C. pyxidata</i> (L.) Hoffm.   |                                |
| <i>C. chlorophaea</i> (Flörke) Sprengel  |                                |
| <i>C. fimbriata</i> (L.) Fries   |                                |
| <i>C. subulata</i> (L.) Wigg.  |                                |
| Subsect. <i>Thallostelides</i>   |                                |
| * <i>C. phyllophora</i>  |                                |
| * <i>C. cervicornis</i> subsp. <i>cervicornis</i>                                    |                                |
| * <i>C. chlorophaea</i>  |                                |
| Sect. <i>Perviae</i> (Fries) Mattick   |                                |
| Subsect. <i>Chasmariae</i> (Achar.) Mattick  |                                |
| Series <i>Furcatae</i> E. Dahl   |                                |
| <i>C. furcata</i> (Hudson) Schrader  |                                |
| Series <i>Squamosae</i> E. Dahl  |                                |
| <i>C. carassensis</i> Vainio s. lat.   |                                |
| <i>C. squamosa</i> (Scop.) Hoffm.  |                                |
| var. <i>squamosa</i>   |                                |
| <i>C. squamosa</i> (Scop.) Hoffm. var. <i>sub-squamosa</i> (Nyl. ex Leighton) Vainio |                                |
| * <i>C. crispata</i> (Achar.) Flotow s. str.   |                                |

western North America. Atranorin was present in most specimens of *C. cervicornis* subsp. *cervicornis* from the Ione Formation sites. It was rare in over 100 specimens of *C. cervicornis* from outside of Amador County. Culberson (1986) discussed the loss of atranorin as a derived trait in the *C. chlorophaea* group, which is closely related to *C. cervicornis* (subsect. *Thallostelides*). The influence of gene flow in populations of lichens on their chemical constituents was demonstrated by Culberson et al. (1988). *Cladonia cervicornis* in the pygmy forest has remained in contact with contiguous populations that range along the Pacific coast of California from the Mexican border to Oregon. Gene flow and the subsequent evolution of derived chemotypes (presence of fumarprotocetraric acid only and loss of atranorin in most individuals), may be inferred for these populations. The Amador County population of *C. cervicornis* has been geographically isolated from coastal populations. Its concomitant



reproductive and genetic isolation may be inferred from its retained primitive chemical characteristics.

Geographic isolation at the Ione Formation sites has influenced the diversity of *Cladonia* species as well as their chemical characteristics. In contrast to the pygmy forest, where 17 species and four subsections are represented, only one subsection and three species are represented at the Amador County sites (Table 1).

The pygmy forest of Mendocino County and the Ione Formation of Amador County are areas where low soil pH is correlated with unique distributions of phanerogams. Cryptogams such as the lichen genus *Cladonia* demonstrate unique patterns of distribution in these areas as well. Vicariance and subsequent isolation on specialized soils has led to speciation and endemism in many vascular plants such as *Arctostaphylos nummularia* and *A. myrtifolia*. Many widely distributed taxa of the genus *Cladonia* are relictual at these localities, and possess primitive characters. Where contact with widespread populations has been maintained, as in coastal populations, derived characters may be observed.

#### ACKNOWLEDGMENTS

I thank Dr. Harry D. Thiers, under whom this work was begun, and Dr. Nancy Carnal for their reading of an earlier version of this manuscript. Thanks to Dr. V. Thomas Parker, who sparked my interest in the Ione Formation. I am grateful to Dr. John W. Thomson for verification of specimens. I thank Dr. Teuvo Ahti for his discussions concerning taxonomic concepts. I am indebted to Barbara Lachelt and Herbert Saylor for access to their collections. I thank the curators of CAS, FH, HSC, LAM, NY, SBM, and SFSU for their assistance. The California Botanical Society is acknowledged for its financial support in the form of a graduate student research fellowship. Dr. Donald H. Pfister is thanked for his comments regarding this manuscript. This paper was presented in part at a graduate seminar in biogeography at Harvard University.

#### LITERATURE CITED

- CULBERSON, C. 1974. Conditions for the use of Merck silica gel 60 F 254 plates in the standardized thin-layer chromatographic technique for lichen products. *J. Chromatogr.* 97:107–108.
- . 1986. Biogenetic relationships of the lichen substances in the framework of systematics. *Bryologist* 89:91–98.
- , W. L. CULBERSON, and A. JOHNSON. 1981. A standardized TLC analysis of the  $\beta$ -orcinol depsidones. *Bryologist* 84:16–29.
- , ———, and ———. 1988. Gene flow in lichens. *Amer. J. Bot.* 75:1135–1139.
- GANKIN, R. and J. MAJOR. 1964. *Arctostaphylos myrtifolia*, its biology and relationship to the problem of endemism. *Ecology* 45:792–808.
- HAMMER, S. 1988. A taxonomic survey of the lichen genus *Cladonia* in California. M.A. thesis, San Francisco State University, San Francisco, CA.
- . 1989. *Cladonia carneola*: two new localities in western North America. *Bryologist* 92:126–127.
- JENNY, H., R. J. ARKLEY, and A. M. SCHULTZ. 1969. The pygmy forest-podosol ecosystem and its dune associates of the Mendocino coast. *Madroño* 20:60–74.



- KRUCKEBERG, A. R. 1969. Soil diversity and the distribution of plants, with examples from western North America. *Madroño* 20:129–154.
- MALACHOWSKI, J. A. 1975. Macrolichens of the pygmy forest. M.S. thesis. Chico State University, Chico, CA.
- MASON, H. H. 1946a. The edaphic factor in narrow endemism I. The nature of environmental influences. *Madroño* 8:209–226.
- . 1946b. The edaphic factor II. The geographic distribution of plants of highly restricted patterns of distribution. *Madroño* 8:241–257.
- McMILLAN, C. 1956. The edaphic restriction of *Cupressus* and *Pinus* in the coast ranges of central California. *Ecol. Monogr.* 26:177–212.
- RAVEN, P. H. and D. I. AXELROD. 1978. Origin of the California flora. *Univ. Cal. Publ. Bot.* 72:1–134.
- SINGER, M. J. and P. NKEDI-KIZZA. 1980. Properties and history of an exhumed Tertiary oxisol in California. *Soil Sci. Soc. Amer. Proc.* 44:587–590.
- STEBBINS, G. L. and J. MAJOR. 1965. Endemism and speciation in the California flora. *Ecol. Monogr.* 35:1–35.
- WHITE, F. J. and P. W. JAMES. 1985. A new guide to microchemical techniques for the identification of lichen substances. *Brit. Lich. Soc. Bull.* 75(Suppl.):1–41.

(Received 19 Jan 1989; revision accepted 9 May 1989.)

---

## NOTEWORTHY COLLECTIONS

### MONTANA

*GOODYERA REPENS* (L.) R. Br. (ORCHIDACEAE).—Judith Basin Co., Little Belt Mts., Sandpoint Cr. of Lost Fork of Judith R., 42 km SW of Stanford, T12N R10E SE¼ sect. 10, 1860 m, 3 Aug 1987, *Phillips 870803-34* (MRC) (verified: J. S. Shelly, P. F. Stickney, MRC). Approximately 200 plants were found in a 400-square-meter area on a north-facing slope in dense shade of an old-growth Douglas-fir/lodgepole pine forest. The site is an *Abies lasiocarpa/Linnaea borealis* habitat type on limestone substrate. The orchids were found in an unburned island in the center of a large 1985 burn, growing in thick mats of the mosses *Drepanocladus uncinatus*, *Hylocomnium splendens*, and *Pleurozium schreberi* (det: J. C. Elliott). Other associated species include *Linnaea borealis*, *Pyrola secunda*, *Galium boreale*, *Clematis columbiana*, *Thalictrum occidentale*, *Smilacina stellata*, *Juniperus communis*, *Pseudotsuga menziesii*, *Abies lasiocarpa*, and *Picea engelmannii*.

*Significance.* Second record for MT. Previously known from a single collection (6 Aug 1980, *J. DeSanto*, GNP) from Glacier National Park near Upper Kintla Lake 370 km northwest of the location reported here. This site is also disjunct by 600 km from next closest known U.S. station in the Black Hills, SD. In addition to MT, western U.S. distribution includes CO, NM, and AZ, but the species is not known from the adjacent states of WY and ID.—H. WAYNE PHILLIPS, Lewis and Clark National Forest, P.O. Box 871, Great Falls, MT 59403.



# A NOTE ON THE GERMINATION AND ESTABLISHMENT OF *PHORADENDRON CALIFORNICUM* (VISCACEAE)

JOB KUIJT

Department of Biological Sciences, University of Lethbridge,  
Lethbridge, Alberta T1K 3M4, Canada

## ABSTRACT

During germination, the radicle of *Phoradendron californicum* elongates greatly, eventually forming a minute disk or wedge from which penetration of the host is effected. Subsequently, the epicotylar pole and the entire radicle wither and die, the young plant having an exclusively endophytic existence for a brief period. All aerial shoots are formed adventitiously from endophytic strands. This pattern of establishment corresponds to that in *Arceuthobium*, but in *Phoradendron* is not known from other species, although a few species in *Phoradendron* and *Viscum* show transitional patterns.

The stage in a mistletoe's life cycle which leads from seed germination to the full establishment of the endophyte is of great biological interest. It is surprising, therefore, that this stage has not been scrutinized in the case of the common desert mistletoe, *Phoradendron californicum* Nutt., even though the interaction of the seedling with its host has received some notice (Cannon 1904; Tinnin et al. 1971). The present note documents some unusual aspects of this early development. Fruits were collected on about 20 May 1982, near Julian, San Diego County, California, the host being *Acacia greggii* A. Gray. The material illustrated in Figure 4 derives from the same locality and host two years earlier.

The most important avian disseminator of *P. californicum* is the Phainopepla, *Phainopepla nitens*, which tends to concentrate eliminated seeds in small clusters on the host branches near the fruiting parasite (Cowles 1936; Crouch 1943). My attention was drawn some years ago to the fact that no erect seedlings could be located even where live host branches were littered with innumerable germinating mistletoe seeds. Furthermore, those seedlings were characterized by an exceedingly long and slender radicle strikingly reminiscent of that of *Arceuthobium* and not at all like the type which one finds in North America and tropical America in other species of *Phoradendron* and in the closely related genus *Dendrophthora* (unpubl. obs.), where radicles tend to be short and the seedlings phanerocotylous. No seedling could be found in which the cotyledons had been withdrawn from the endosperm.



## OBSERVATIONS

With such questions in mind, I closely followed germination on several potential but unproven host species (*Cassia* sp., *Callistemon* sp., *Nerium oleander* L.) for up to 18 months in the University of Lethbridge greenhouse. Unfortunately, none of the numerous seedlings became established, and the complete transition from the independent stage to parasitic dependence could thus not be followed. Radicles, both in the field and in the greenhouse, are generally bright red and uniformly 0.3 mm in diameter. They often grow out in a nearly straight fashion until about 3 mm long (Fig. 1). Since most seeds become attached to the host in a sideways manner, the initial growth-direction tends to parallel the host surface. Eventually, a hinge-like movement apparently localized just outside the endosperm brings the tip of the rigid radicle into contact with the host, where a disk is formed (Fig. 2). The form of the disk is adapted to whatever space is available at that point, and may thus be more like a flattened wedge or peg. When the seed initially adheres so as to point towards the host, the growth pattern tends to be more regular in that the radicle advances towards the host surface. Conversely, if the seed becomes attached by the end opposite the radicle, the latter curves immediately upon emergence and grows towards the host surface. In one instance, the radicle reached a length of 7 mm and lived for 18 months (Fig. 3), but field conditions probably do not allow such records.

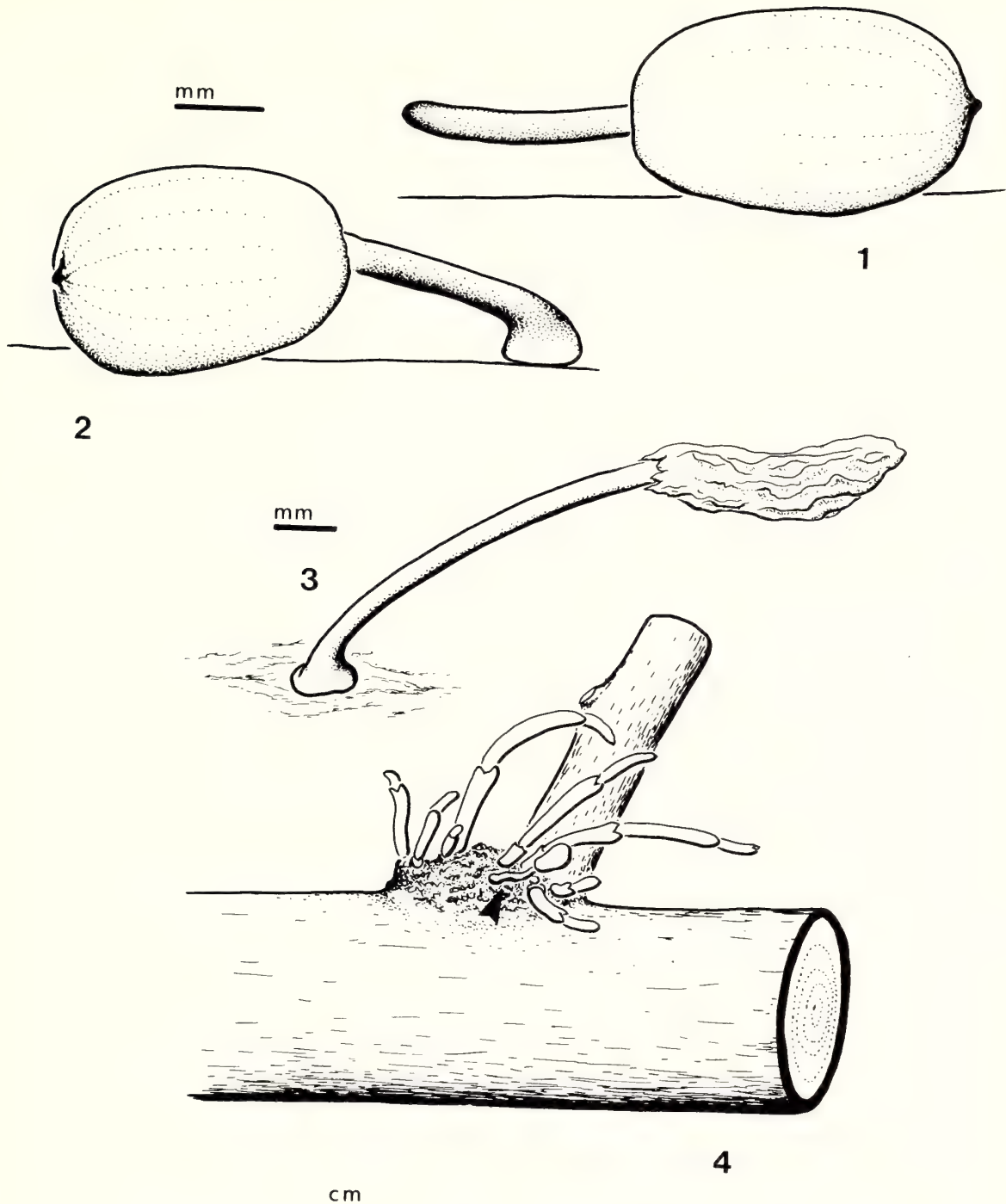
Fortunately, young specimens were collected which unequivocally showed the subsequent development (Fig. 4). The epicotylar end, indeed, does not emerge from the endosperm, and all external portions shrivel up and die after penetration has occurred. In the meantime, the endophytic strands expand into the host tissues and produce a cluster of aerial shoots near the original point of entry. I have no information on how long a period passes before flowering takes place, but I assume this to be not before the second growing season.

In other cases, individual shoots were noted as they emerged from a vigorous endophytic strand visible by a line of raised host bark radiating out from an older plant. The vigor and frequency of shoots which emerge are likely to be a function of the size of the host branch and perhaps host species.

## DISCUSSION

The young mistletoe radicle has often been described as being negatively phototropic, thus curving directly towards the host branch no matter on what side it is attached (Kuijt 1969), after which the haustorial disk is formed and the cotyledons and epicotyl are withdrawn from the endosperm. This is undoubtedly true for the great majority of mistletoes (see, for example, Kuijt 1982). It is notewor-





FIGS. 1–3. Germination stages of *Phoradendron californicum*, respectively of the following ages: 1, 1, and 18 months. 1. The radicle has grown out straight, parallel to the host surface. 2. The entire radicle, while still straight, has been lowered, the haustorium forming at the tip. 3. The haustorial disk is attached to the host surface, and the exhausted endosperm has been lifted by the epicotylar pole of the seedling. Germination in greenhouses, University of Lethbridge. 4. The earliest shoots formed of a vigorous, young individual of *P. californicum*, collected on *Acacia greggii*, Julian, California. The original seedling still adheres (arrow) but is dead.

thy, however, that Tubeuf (1923, p. 414) already noted an insensitivity of the radicle to external growth stimuli in the early germination stages of *Viscum album* L., a situation which seems to be comparable to that in *Phoradendron californicum*. Clearly, the rad-



icle passes through physiologically very different stages during germination.

Vegetative reproduction from endophytic strands is common in many Viscaceae, including some other species of *Phoradendron* like *P. villosum* Engelm., some *Viscum* species (Tubeuf 1923; Kuijt 1986) and *Dendrophthora* (Kuijt 1987b), and the entire genus *Arceuthobium* (Kuijt 1960). However, the complete *replacement* of the normal shoot system derived from the epicotyl by adventitious shoots has not before been reported in *Phoradendron*. This pattern of establishment has earlier been called the *Arceuthobium* pattern (Kuijt 1986), since it has long been known for that genus. It has recently also been shown to occur in *Viscum minimum*, but there appears to be still in a transitional stage from a normal pattern in that the plant does not entirely "withdraw" into the host upon entry, but rather leaves an external haustorial cushion (the disk) from which some of the early aerial shoots are formed (Kuijt 1986). The *Arceuthobium* pattern has evolved independently in a single species of Loranthaceae (*Tristerix aphyllus* (DC.) Barlow & Wiens; Reiche 1904; Mauseth et al. 1985), and is possibly present in *Lepidoceras peruvianum* Kuijt of Eremolepidaceae (Kuijt 1988). It may also be expected in the genus *Phacellaria* (Santalaceae) (Kuijt 1969). This represents at least 3 documented cases of remarkably parallel evolution.

In one group of *Phoradendron* species, all of which are hyperparasitic on other mistletoes, a separate transitional pattern has evolved (Kuijt 1987a). While we do not know anything about the seedlings of this group, it is clear that at an early stage a haustorial cushion is formed very much like that of *Viscum minimum*. It is from this cushion that most (or perhaps all) shoots originate. Whether the primary shoot, and therefore the epicotyl of these species function normally remains to be established. Sprouting from the haustorial disk may, of course, be present in other species as well but is likely to be infrequent. It has not been observed in *P. californicum*.

In summary, then, I have shown that the seedling of *P. californicum* is cryptocotylar and of the *Arceuthobium*-type of development in that all aerial shoots are adventitious, the primary apical shoot meristem aborting. The "seed coat" of this mistletoe forms a shiny capsule around the living endosperm, and it is worth mentioning that the only North American member of Loranthaceae s.s. to become similarly adapted to deserts, *Psittacanthus sonora* (S. Watson) Kuijt, has evolved a comparable sheathing capsule and cryptocotylar germination pattern (Kuijt 1973). In fact, these two mistletoes in Baja California may be found together and even in hyperparasitic combination (Kuijt 1971). The above-mentioned *Viscum minimum* also is a distinctively xeric species, being parasitic upon extremely succulent *Euphorbia* species in South Africa, as is *Tristerix aphyllus*



on several desert cacti in Chile. The desert environment thus seems to have brought about parallelisms in the pattern of establishment of diverse mistletoes. The germination pattern in *Arceuthobium*, similarly, may point to an early evolutionary origin in a desert environment.

#### ACKNOWLEDGMENTS

I am indebted to Mr. Wayne Armstrong, Palomar College, for assistance in the field. Financial support originated from the Natural Science and Engineering Research Council of Canada.

#### LITERATURE CITED

- CANNON, W. A. 1904. Observations on the germination of *Phoradendron villosum* and *P. californicum*. Bull. Torrey Bot. Club 31:435–443.
- COWLES, R. B. 1936. The relation of birds to seed dispersal of the desert mistletoe. Madroño 3:352–356.
- CROUCH, J. E. 1943. Distribution and habitat relationships of the Phainopepla. Auk 60:319–333.
- KUIJT, J. 1960. Morphological aspects of parasitism in the dwarf mistletoes (*Arceuthobium*). Univ. Calif. Publ. Bot. 30:337–436.
- . 1969. The biology of parasitic flowering plants. Univ. Calif. Press, Berkeley & Los Angeles.
- . 1971. Transfer of *Phrygilanthus sonora* to *Psittacanthus*. Madroño 21: 13–14.
- . 1973. Further evidence for the systematic position of *Psittacanthus sonora* (Loranthaceae). Madroño 22:177–185.
- . 1982. Seedling morphology and its systematic significance in Loranthaceae of the New World, with supplementary comments on Eremolepidaceae. Bot. Jahrb. 103:305–342.
- . 1986. Observations on establishment and early shoot emergence of *Viscum minimum* (Viscaceae). Acta Bot. Neerl. 35:449–456.
- . 1987a. Novelties in Mesoamerican mistletoes (Loranthaceae and Viscaceae). Ann. Missouri Bot. Gard. 74:511–532.
- . 1987b. Miscellaneous mistletoe notes, 10–19. Brittonia 39:447–459.
- . 1988. Monograph of the Eremolepidaceae. Syst. Bot. Monogr. 18:1–60.
- MAUSETH, J. D., G. MONTENEGRO, and A. M. WALCKOWIAK. 1985. Host infection and flower formation by the parasite *Tristerix aphyllus* (Loranthaceae). Can. J. Bot. 63:567–581.
- REICHE, K. 1904. Bau und Leben der chilenische Loranthacee *Phrygilanthus aphyllus*. Flora 93:271–297.
- TINNIN, R. O., C. L. CALVIN, and R. L. NULL. 1971. Observations on the establishment of seedlings of *Phoradendron californicum* on *Prosopis juliflora*. Phytomorphology 21:313–320.
- TUBEUF, C. 1923. Monographie der Mistel. Oldenbourg, Berlin.

(Received 24 Oct 1988; revision accepted 11 Apr 1989.)



# REDUCTION IN LIGHT REFLECTANCE OF LEAVES OF *ENCELIA DENSIFOLIA* (ASTERACEAE) BY TRICHOME WETTING

DANIEL F. HARRINGTON and CURTIS CLARK<sup>1</sup>  
Biological Sciences, California State Polytechnic University,  
Pomona, CA 91768

## ABSTRACT

*Encelia densifolia* is a desert shrub endemic to a single mountain range in the central western portion of the Baja California peninsula. When dry, its pubescent leaves reflect about as much light as other pubescent *Encelia* species, such as *E. actoni* and *E. palmeri*, although not as much as the densely tomentose *E. farinosa*. When the leaves are wet, their trichomes absorb water, and reflectivity is decreased to a level comparable to nearly glabrous *Encelia* species, such as *E. californica* and *E. frutescens*. This response to wetting is likely to be advantageous to the plants; they inhabit a region of summer fogs, where light intensity and air temperature are reduced and relative humidity is increased by the same conditions that reduce leaf reflectance.

## RESUMEN

*Encelia densifolia* es un arbusto del desierto, endémico a una sola sierra en la comarca occidental del centro de la península de Baja California. Cuando secas, sus hojas pubescentes reflejan casi tanto como otras especies pubescentes de *Encelia*, tal como *E. actoni* y *E. palmeri*, aunque no tanto como la muy tomentosa *E. farinosa*. Cuando las hojas son mojadas, sus tricomas absorben el agua, y la reflectividad disminuye a un nivel análogo a especies pelonas, tal como *E. californica* y *E. frutescens*. Esta respuesta a lo mojando es probable que será ventajosa a las plantas. Habitan una comarca de nieblas estivales, donde la intensidad de la luz y la temperatura del aire se reducen y la humedad relativa se aumenta por las mismas condiciones que reducen la reflectividad de las hojas.

A number of studies have been conducted in recent years concerning the adaptive nature of leaf pubescence. The genus *Encelia* has been one of the most intensely investigated, particularly *E. farinosa* and the role the pubescence plays in the adaptation of this species to its desert climate (Ehleringer and Clark 1988, and references cited therein). Ehleringer and others have shown that leaf hairs are important to the success of the plants in their hot, dry habitat, because pubescence increases reflection of solar radiation, lowering leaf temperatures and rates of water loss (Ehleringer and Clark 1988).

A newly described species of *Encelia*, *E. densifolia* Clark & Kyhos, is similar to other species of the genus in that a dense pubescence of multicellular uniseriate hairs covers both surfaces of the leaves

<sup>1</sup> Correspondence should be addressed to this author.



(Clark et al. 1988). Although the trichomes form a continuous cover over the surface of the leaves, we have found that the leaves are not as reflective as those of other species such as *E. palmeri* and *E. farinosa* (Ehleringer and Clark 1988). Moreover, unlike those of *E. farinosa*, the trichomes of *E. densifolia* absorb water easily and in doing so lose most of their reflective capacities. *Encelia densifolia* is endemic to canyons in the Picachos de Santa Clara, Baja California Sur, México, where fog is common in the summer, and Clark et al. (1988) suggested that the loss of reflectivity of the leaves could be an adaptation to increase light capture on foggy days.

Our purpose in this study was to compare the differences in leaf light reflectance between dry and wet leaves of *Encelia densifolia*, to compare these results with those of the sympatric and well-studied species *E. farinosa*, and finally to determine what physical features of the trichomes of these two species account for the differences.

#### MATERIALS AND METHODS

All studies were conducted with plants grown from seed and maintained outdoors at California State Polytechnic University, Pomona (methods follow Kyhos et al. 1981). All the seeds were obtained from plants growing in native habitats in México, in the state of Baja California Sur (vouchers at CSPU): *Encelia densifolia*—Picachos de Santa Clara, 13.6 mi NW of San Ignacio—Abreojos road at a point 24.7 mi NE of Punta Abreojos, 24 Mar 1981, accession 184, Clark 585. *Encelia farinosa*—Pemex station on Mex Hwy 1 at San Ignacio, 23 Mar 1981, accession 183; S of Bahía Concepción at Microondas Rosarito, 25 Mar 1981, accession 186; S end of Bahía Concepción, near the beach, 27 Mar 1981, accession 190.

We measured leaf reflectance by placing the individual leaves (adaxial side exposed) in the sample slot of the integrating sphere of a Shimadzu/Bausch & Lomb Spectronic 210 U.V. recording reflectance spectrophotometer. Reflectances were measured at the violet (425 nm) and red (670 nm) peaks of the photosynthetic action spectrum (Jensen and Salisbury 1984, p. 81). Magnesium oxide powder (Wako Pure Chemical Industries, supplied with the integrating sphere) was used as a reference. To insure accuracy of the reference, two blanks were prepared and calibrated against each other; if either deviated from the range of 99%–101% compared to the other, both were discarded, and new references were prepared.

Ten ontogenetically mature leaves were selected at random from each of ten plants of *Encelia densifolia* during the period from 7 to 13 October, 1986, and six leaves were used from each of twelve plants of *E. densifolia* on 2 February 1987. During the fall, individual leaves of *E. densifolia* were sometimes not large enough to cover the opening in the integrating sphere (18 mm diameter); in those



cases, two leaves were overlapped, giving sample sizes less than 10. For comparison, ten leaves from each of three plants of *E. farinosa* were taken in 2 February. For each leaf, reflectance was measured, the leaf was wetted with deionized water, excess water was allowed to drain, and reflectance was measured again. The same wetting procedure was used to generate five reflectance spectrograms over the range of 400–700 nm.

We tested for the presence of cuticle on the trichomes of both species with Sudan Black B (a histochemical stain for lipids) used on freehand sections and epidermal peels of fresh leaves.

We estimated the rate of water absorption by the trichomes by dropping two drops of water in separate locations on each of four leaves of both species, and measuring the elapsed time until each drop was absorbed. To assess the effect of cuticle removal, we performed three experiments. In each, leaves were dipped in 95% acetone for varying times, allowed to air-dry, and the absorption rate test was performed as described above. In the first experiment, four leaves of each species were dipped for 1 sec while still attached to the plants, and allowed to recover for 86.4 ksec (1 day). *Encelia densifolia* leaves were not used in the other two experiments, since water absorption in the first experiment was nearly instantaneous. In the second experiment, four leaves were removed from the plant, dipped in acetone for 1 sec, and measured immediately upon drying. In the third experiment, five leaves were removed from the plant, dipped for 300 sec, and measured immediately upon drying. In all cases, timing of the absorption of an individual water drop was discontinued if it had not been absorbed after 60 sec.

Fog simulation was accomplished with a Fogg-It "Waterfog" Nozzle, rated at one-half gallon per minute (31.5 ml/sec). We sprayed the fine mist upwind from the plants to mimic actual fog conditions. Effects on the leaves were assessed visually.

All statistical analyses were performed with the MINITAB statistical package on the California State University Central Cyber System computer.

## RESULTS

We found significant differences in reflectance between wet and dry leaves of *Encelia densifolia*. Over the entire spectrum from 400 nm to 700 nm, the reflectance of wet leaves was 50–60% of that of dry leaves (Fig. 1), whereas in *E. farinosa* there was no appreciable change (data not shown). At both 425 nm and 670 nm, wet *E. densifolia* leaves were significantly less reflective than dry leaves, for both the fall and winter samples. In contrast, there were no significant differences between wet and dry *E. farinosa* leaves at both wavelengths (Fig. 2). These results also held for each individual plant of both species (two-sample t-test,  $p < 0.05$ ).



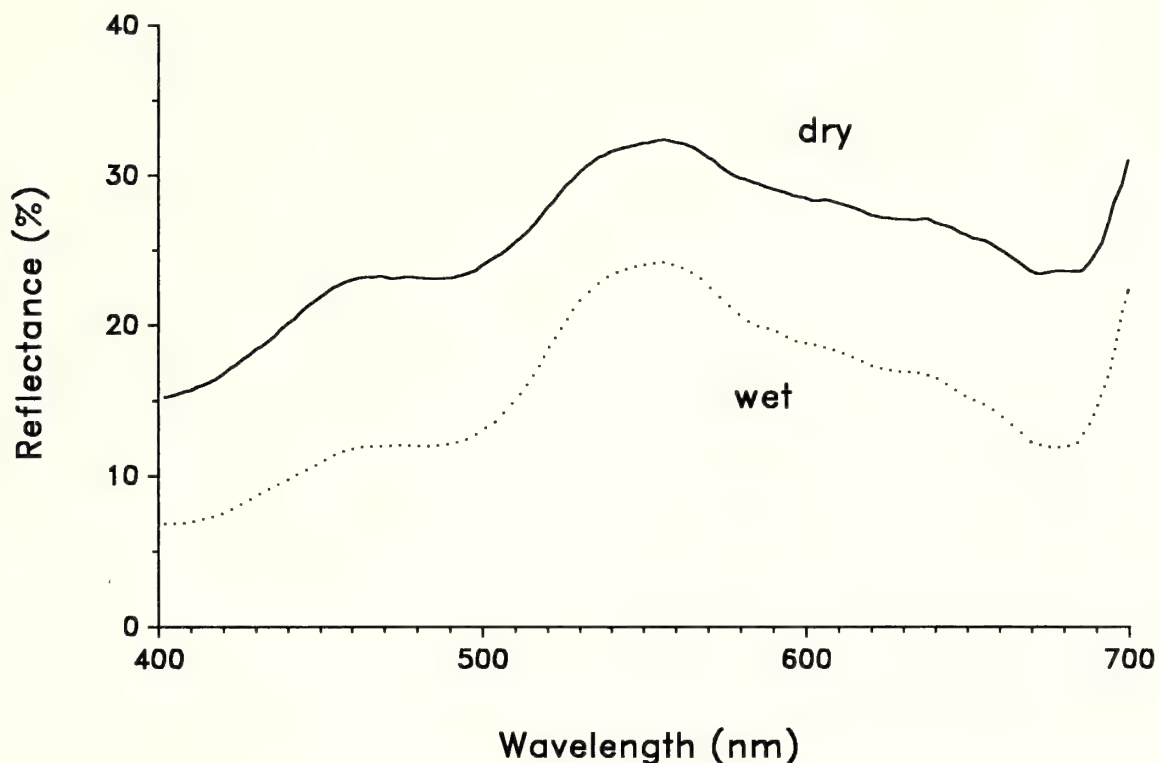


FIG. 1. Reflectance spectra of a representative leaf of *E. densifolia*, before and after wetting of the trichomes.

Although it was not our intent to assess seasonal changes in reflectivity, because the plants are freely watered in cultivation, we did find differences between the October and February samples. At 425 nm, dry leaves were significantly more reflective in October (two sample t-test,  $p < 0.05$ ), but there was no significant difference between wet leaves. At 670 nm, both wet and dry leaves were significantly more reflective in February ( $p < 0.01$ ).

In the wetting experiment, most areas on an untreated leaf of *E. densifolia* were saturated by water in under 1 sec. With untreated *E. farinosa* leaves, saturation generally had not occurred at 60 sec, when measurement was discontinued, and on one leaf neither water droplet had been absorbed after more than 2 ksec. Even when such long wetting times are recorded as 60 sec, there is a significant difference in wettability between the two species (Mann-Whitney U-test,  $p < 0.0001$ ).

Although cuticle of the epidermal cells of both species was stained by Sudan Black B, the trichomes of both species remained generally unstained, with only a very few of the basal cells staining. Wettability decreased in acetone-dipped leaves, however, to the extent that *E. farinosa* leaves treated for five minutes with acetone were, with the exception of a single leaf, just as absorbent as leaves of *E. densifolia* (Fig. 3).

As expected, simulated fog caused an immediate reduction in leaf reflectance of *Encelia densifolia*; the fine water droplets were quickly absorbed by the trichomes. With *E. farinosa*, on the other hand, the



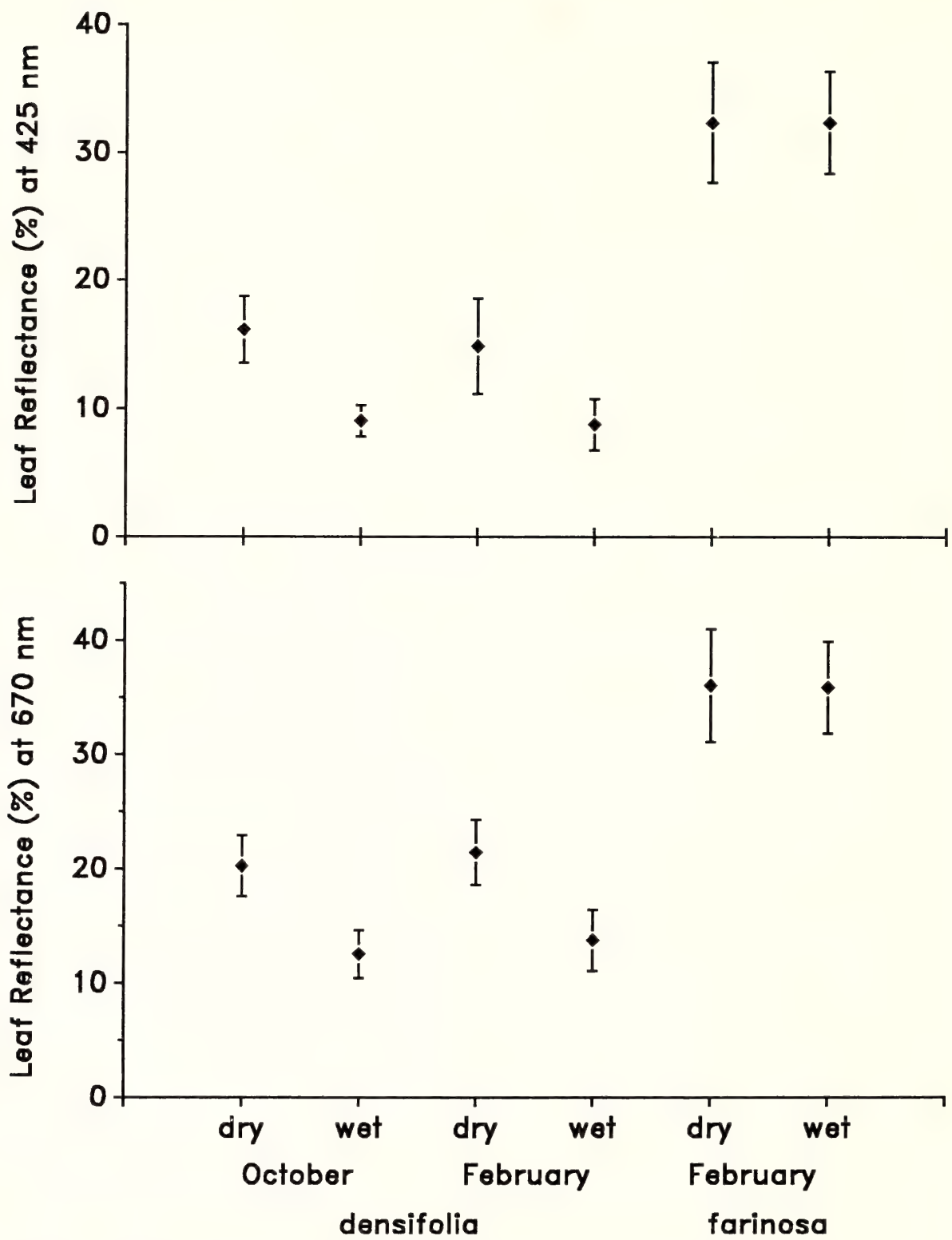


FIG. 2. Reflectance of wet and dry leaves of *E. densifolia* and *E. farinosa*. Means are marked by diamonds, and error bars represent  $\pm 1$  SD. Means were significantly different (two-sample t-test,  $p < 0.001$ ) for wet and dry *E. densifolia* leaves in both seasons.



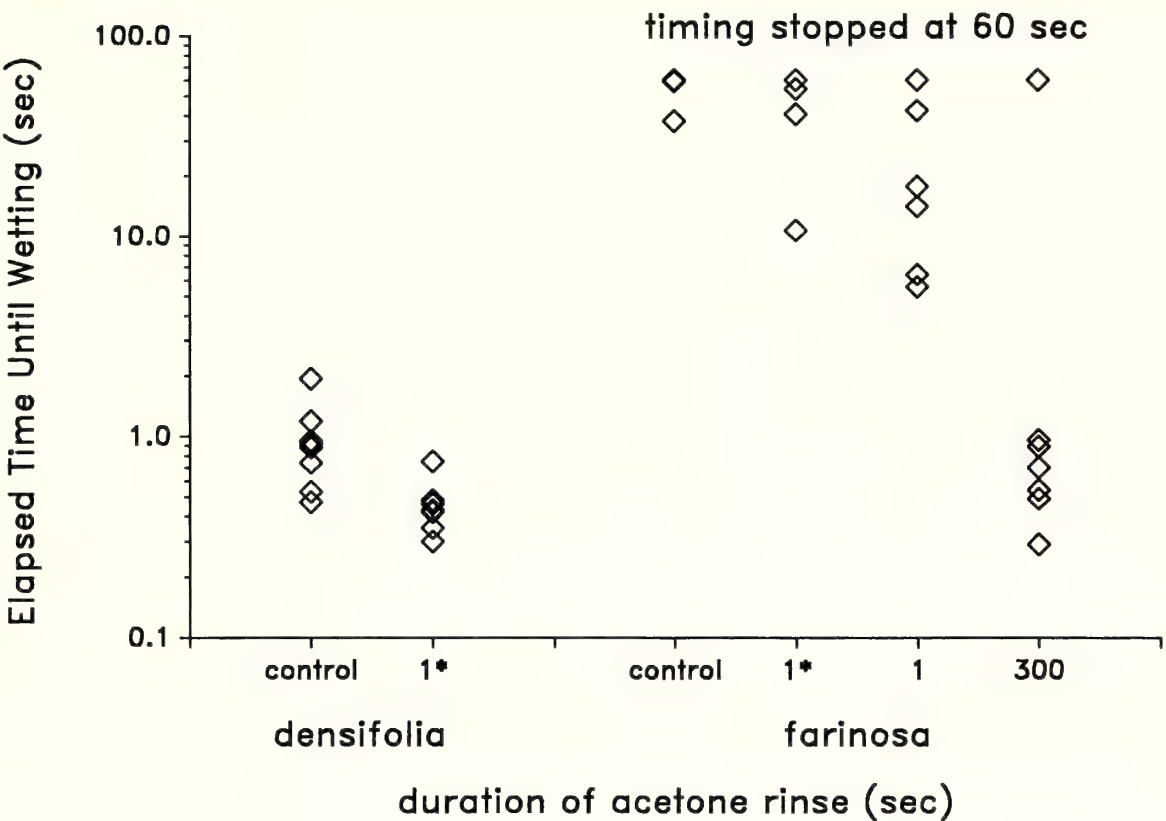


FIG. 3. Univariate scatterplot of elapsed time until a drop of water was absorbed by the leaf trichomes of *E. densifolia* and *E. farinosa* (see text for explanation).

water droplets beaded up on the surface of the trichome layer, eventually coalescing and running off the leaf.

DISCUSSION

When dry, the leaves of *Encelia densifolia* are as reflective as other pubescent-leaved *Encelia* species, such as *E. actoni* and *E. palmeri*. When they are wet, their reflectance decreases to a level comparable to nearly glabrous species, such as *E. californica* and *E. frutescens* (Ehleringer and Clark 1988). The well-studied *E. farinosa*, which is sympatric with *E. densifolia*, shows no changes in reflectance between dry and wet leaves, and in fact the leaf trichomes are not wettable.

Although histochemical staining showed no cuticle layer on the trichomes of either species, the hydrophobic nature of *E. farinosa* trichomes was sharply reduced by an acetone rinse. This is consistent with the removal of cutin or some other lipophilic substance.

We believe these differences can be accounted for by the unusual environmental conditions in the habitat of *E. densifolia*. The region is characterized by frequent fog from the Pacific Ocean during the summer, especially in May, June, and July, the driest months of the year (Wiggins 1980). During fog conditions the leaf trichomes be-



come wet and the leaves lose most of their reflectivity. This decreased reflectivity comes at a time when it is most beneficial (light intensity is reduced by the fog) and least harmful (air temperatures are reduced and relative humidity is very high).

In the same environment, the leaves of *E. farinosa* maintain their reflectance regardless of atmospheric conditions. That *E. farinosa* and pubescent species of other genera thrive in the area is an indication that the adaptation exhibited by *E. densifolia* is not a general requirement. On the other hand, *E. farinosa* is the most widely distributed species in the genus (Shreve and Wiggins 1964), while *E. densifolia* is not found outside of the fog zone. Although there are undoubtedly other factors involved in this restriction, we believe that the unique adaptation of *E. densifolia* helps it survive as a relict in a generally unsuitable region, rather than giving it an advantage over other desert shrub species.

#### ACKNOWLEDGMENTS

This study represents a Senior Project carried out by D. F. H. at California State Polytechnic University, Pomona, in partial fulfillment of the requirements for the Bachelor of Science degree from California Polytechnic State University, San Luis Obispo. Research was supported in parts by grants to C. C. from the Cal Poly Kellogg Unit Foundation and the Affirmative Action Faculty Development Program. We thank L. M. Blakely and J. A. Tres for their assistance.

#### LITERATURE CITED

- CLARK, C., D. W. KYHOS, and N. CHAREST. 1988. A new *Encelia* (Asteraceae: Heliantheae) from Baja California. *Madroño* 34:10–15.
- EHLERINGER, J. and C. CLARK. 1988. Evolution and adaptation in *Encelia* (Asteraceae). Pp. 221–248 in L. D. Gottlieb and S. K. Jain (eds.), *Plant evolutionary biology*. Chapman & Hall, London.
- JENSEN, W. A. and F. B. SALISBURY. 1984. *Botany*, 2nd ed. Wadsworth Publishing Company, Belmont, CA.
- KYHOS, D. W., C. CLARK, and W. C. THOMPSON. 1981. The hybrid nature of *Encelia laciniata* (Compositae: Heliantheae) and control of population composition by post-dispersal selection. *Syst. Bot.* 6:399–411.
- SHREVE, F. and I. L. WIGGINS. 1964. *Vegetation and flora of the Sonoran Desert*. Stanford Univ. Press.
- WIGGINS, I. L. 1980. *Flora of Baja California*. Stanford Univ. Press, Stanford, CA.

(Received 14 Dec 1988; revision accepted 30 May 1989.)



# THE *ARISTIDA CALIFORNICA-GLABRATA* COMPLEX (GRAMINEAE)

JOHN R. REEDER

Herbarium, University of Arizona,  
Tucson, AZ 85721

RICHARD S. FELGER

Office of Arid Land Studies, University of Arizona,  
Tucson, AZ

## ABSTRACT

Two closely related taxa of the *Aristida californica* complex differ primarily in having either pubescent or glabrous culms. The pubescent form, *A. californica*, was described by Thurber in 1880. Eleven years later plants with glabrous culms were named *A. californica* var. *glabrata* by Vasey. Hitchcock elevated Vasey's variety to species rank in 1924, a disposition which has been accepted generally by subsequent botanists.

To determine whether these taxa merit specific rank, collections from throughout the ranges of both were analyzed utilizing five spikelet characters. Measurements of length of both glumes, lemma, awn column, and free awns revealed a high degree of overlap; for the lemma, the overlap was complete. Chromosome counts ( $2n=22$ ) are reported for the first time for collections of both taxa. Even though their geographical ranges are reasonably separate, and they tend to occur at different elevations, we conclude that it is more realistic to treat them as varieties of a single species.

## RESUMEN

Dos taxa cercanas, pertenecientes al complejo de *Aristida californica*, difieren principalmente en la superficie del culmo; una es pubescente y la otra es glabra. La forma pubescente, *A. californica*, fué descrita por Thurber en 1880. Once años después, plantas con culmos glabros fueron llamadas *A. californica* var. *glabrata* por Vasey. La última taxon fué elevada al nivel de especie por Hitchcock en 1924.

Para determinar la categoría más correcta, hemos analizada colecciones de la distribución entera para ambas taxa, con la base de cinco caracteres de la espiguilla. Las medidas de longitud de ambas glumas, la lemma, la columna de las aristas, y las aristas libres, revelaron un alto grado de traslapo; para la lemma esté fué completo. Se reporta por primera vez el número cromosómico ( $2n=22$ ) para las ambas taxa. Aunque sus distribuciones geográficas están separadas razonablemente y, en general, ellas tienden a ocupar altitudes diferentes, es nuestra opinión que una mejor taxonomía resulta cuando éstas taxa estan consideradas como dos variedades de una sola especie.

*Aristida californica* was described by Thurber (1880), who cited collections from the Colorado Desert (*Schott*) and Fort Mohave (*Cooper*). There is no problem regarding the identity of the plant, which is described as being tufted, the culms pubescent, branched above, and with the awn column articulated with the lemma body,



from which it separates at maturity. Thurber stated: "It is the only species of the section with articulated, caducous awns (*Arthratherum*) thus far found in North America." This comment is not strictly correct, but Thurber can be forgiven. Although two other North American species, *A. tuberculosa* Nutt. (1818) and *A. desmantha* Trin. & Rupr. (1842), have the characteristics of the section, this fact had not been recognized when Thurber described *A. californica* in 1880.

The section *Arthratherum* was established by Reichenbach (1828), based on the genus *Arthratherum* P. Beauv. (1812). Neither Reichenbach nor Trinius and Ruprecht (1842), who monographed the genus, had recognized either *A. tuberculosa* or *A. desmantha* as belonging to the section. Moreover, Trinius and Ruprecht indicated that members of the section *Arthratherum* are confined to Africa, Asia, and Australia. In that work we find *A. tuberculosa* and *A. desmantha* listed under "§.I. *Aristida* (genuina)." [=Sect. *Aristida*].

Hitchcock (1924) seems to have chosen the Cooper specimen as "lectotype," indicating that it is in the U.S. National Herbarium. Among the specimens he cites, one finds: Fort Mohave, *Cooper 2217*. Moreover, Henrard (1926) states that a fragment of the specimen collected by Dr. Cooper "was kindly received from Prof. Hitchcock." An illustration of *Aristida californica* in Henrard's revision (p. 66) bears the caption: "*From cotype (Fort Mohave, Dr. Cooper 2217).*" Neither Hitchcock nor Henrard mentions having examined a Schott collection. Although Hitchcock did not specifically state he was choosing the Cooper specimen as lectotype, it is clear that he considered it to be "type material." To prevent any future ambiguity regarding the type of this species, we here designate *Cooper 2217* (US-81008) as lectotype of *Aristida californica* Thurber.

Ten years after the publication of *Aristida californica*, Vasey (1891) described a form with glabrous culms, giving it the name var. *glabrata*. It was based on a collection made by T. S. Brandegee at San José del Cabo, Baja California Sur, Mexico, in 1890. Vasey noted that along with the glabrous culms, this taxon differs from the type [*A. californica*] in its larger size, more spreading and branching habit and shorter-awned flowering glumes [lemmas], yet appears to be too near for a new species.

In his revision of *Aristida*, Hitchcock (1924) elevated Vasey's var. *glabrata* to the rank of species. He gave a complete description of the taxon, and noted that it differs from *A. californica* in the glabrous culms, shorter awn column, and longer, more densely flowered panicles. This transfer has been accepted, without comment, by all subsequent botanists. The key character has been pubescent versus glabrous culms, although differences in glume and awn column length are frequently mentioned.

In the same publication, Hitchcock (1924) described a third mem-



ber of Sect. *Arthratherum*, *A. peninsularis*, based on *Palmer 501* collected in Nov 1887 at Bahía de Los Angeles, Baja California Norte, Mexico. It was said to have pubescent culms like *A. californica*, but to differ in being annual, and having larger glumes, lemmas, and awns. Henrard (1926) accepted this species without expressed reservations, as have most other botanists. The sole exception is Gould and Moran (1981), who treat it as a synonym of *A. californica*. They comment that since no distinctly annual plants have been found (in the type locality), *A. peninsularis* must be only an annual appearing form of *A. californica*. We quite agree with this conclusion; all plants of this complex, from any area, are apparently perennial, although they may flower during their first year of growth. Regarding Hitchcock's statement that the spikelet parts are larger in his *A. peninsularis*, with the exception of the lemma (which he gives as "about 8 mm"), we found his measurements fall well within the range we determined for *A. californica*. We examined several specimens from the type locality and none had lemmas longer than 7 mm. We did not see the type.

The present study addresses the question of whether or not the two taxa, *Aristida californica* and *A. glabrata*, are sufficiently distinct to merit specific designation. Vegetatively, the plants exhibit no important differences except for the culms, which are completely glabrous or variously pubescent. The indument, when present, may be rather long and somewhat matted, or extremely short. Various gradations between these two extremes are encountered when a large suite of specimens is examined. Some culms which are devoid of hair may be quite scabrous and, therefore differ but slightly in appearance from others with very short hairs. Nevertheless, one experiences little difficulty in scoring plants as either "glabrous" or "pubescent," and this reasonably consistent feature has been the key character used to separate the two taxa. The basis for naming herbarium specimens also, obviously has been this one feature, and little importance seems to have been placed on whether the hairs are long or short. Along with the pubescent or glabrous culms, authors frequently indicate slight differences in lengths of glumes, and especially the awn column, and free awns. Thus Hitchcock (1951) states that the awn column in *A. californica* is 15 to 20 mm long in contrast to that in *A. glabrata* which he indicates is 6 to 14 mm. In Gould and Moran (1981) the awn length in *A. californica* is said to be 2.5 to 4.5 cm versus 1.5 to 4 cm in *A. glabrata*.

## METHODS

At ARIZ there is a rather large collection representing this complex, which includes gatherings made by both authors over a period of years. In addition, specimens were borrowed from ASU, CAS-



DS, RSA-POM, SD, and UC-JEPS. Our sample consisted of 145 plants with some pubescence on the culms, and 84 in which the culms were completely glabrous. Because plants of the two taxa are very similar vegetatively, we focused on the spikelet: glumes, lemma, awn column, and free awns. To determine the amount of variability in size of spikelet parts on a single individual, we measured ten spikelets on each of four specimens—two with pubescent culms and two with glabrous culms. Care was taken to select spikelets which we judged to be mature, as evidenced by fully developed caryopses within the lemma. Summary statistics were calculated for the 229 specimens, using mean, standard deviation, standard error of the mean, and skewness. Some field work was carried out especially for this study, primarily to gain more information on range and to collect cytological material.

### RESULTS

Among the specimens borrowed from UC-JEPS we found two types. One of these was *Cooper s.n.* collected at Fort Mohave in 1860-61 (UC-37301). This is one of the two collections cited by Thurber in his original description of *Aristida californica* and is thus a syntype; the specimen at US was designated as lectotype earlier in this paper. UC-37301 is, therefore, an isolectotype of *A. californica* Thurb. This specimen has moderately “woolly” culms, but the hairs are not as dense and long as in many other examples of this species. The first glume measures 7–9 mm, the second ca. 15. The lemma is 6.5–7 mm, with a column 14–15 mm, and the awns are 3–4 cm in length.

An apparent isotype of *Aristida californica* var. *glabrata* Vasey is UC-121421. This specimen was collected by T. S. Brandegee (*s.n.*) at San José del Cabo, Baja California Sur, Mexico, 1 Oct 1890. [The Chase Index cites this collection as *Brandegee 34.*] The culms of the UC plant are completely glabrous. The first glume measures 5 mm in length; the second ca. 10 mm. The lemma is 6–6.5 mm, with a column ca. 8 mm, and awns only ca. 2 cm. Clearly, plants representing the types of these two taxa exhibit other differences besides pubescent versus glabrous culms. In var. *glabrata* the glumes are somewhat shorter, and this is also true for the awn column and the spreading awns.

Table 1 summarizes the results obtained from measuring spikelet parts on a single individual; Table 2 presents the data from all specimens studied, and this information is also shown in graphic form in Figure 1.

### CHROMOSOMES

Since we found no published chromosome numbers for members of this complex, along with collecting herbarium specimens, one of



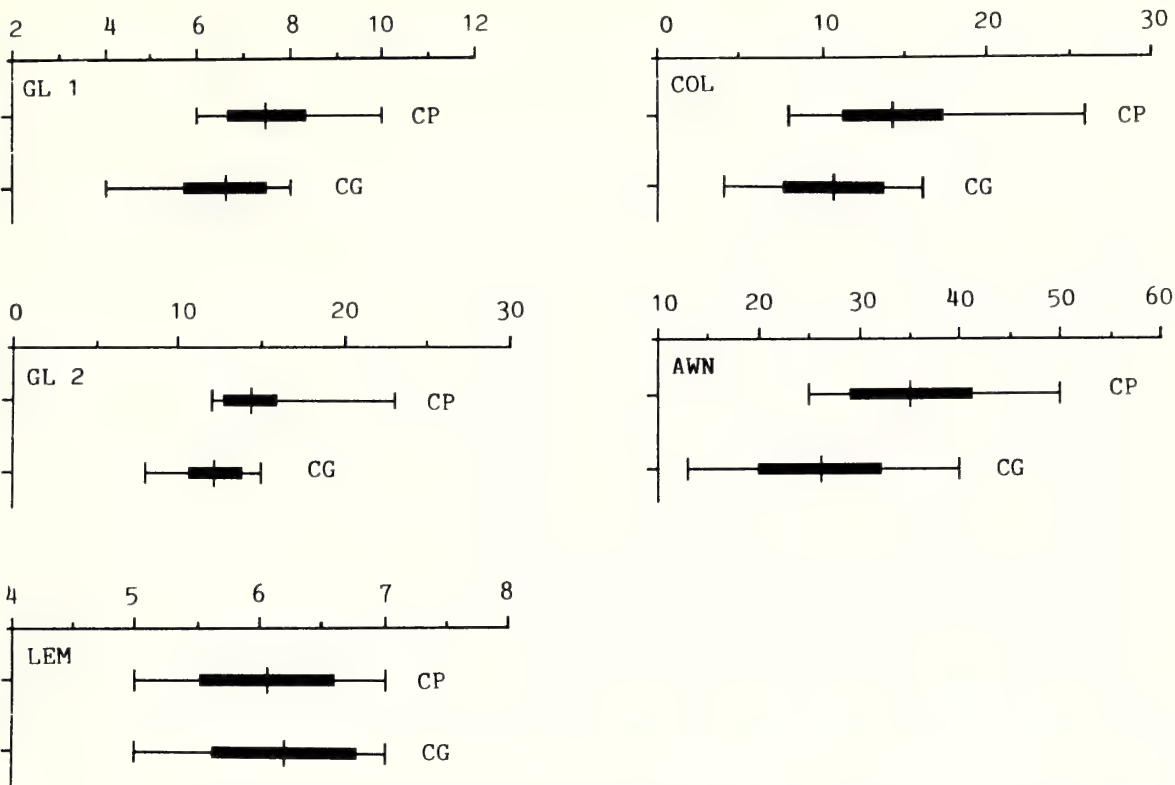


FIG. 1. Summary of measurements in mm of glume 1, glume 2, lemma, awn column, and free awn for the two taxa of the *Aristida californica* complex. Plants with pubescent culms (CP); those with glabrous culms (CG). The diagrams illustrate the range, mean, and the mean  $\pm$  1 standard deviation.

us (Reeder) preserved young inflorescences in the standard 3:1 absolute alcohol–acetic acid mixture for cytological examination. The anthers were later squashed in aceto-carmin. Whether or not the plants had pubescent or glabrous culms, all were determined to be diploid ( $2n=22$ ). The collections are listed below. Collection numbers are those of John R. and Charlotte G. Reeder. Vouchers are at ARIZ.

*Aristida californica* Thurb. var. *californica*: USA. AZ: Pima Co., Cabeza Prieta Natl. Wildlife Refuge, 180 m, 5 Mar 1977, 6835; CA: Imperial Co., 20 km W of Glamis along CA-78, sea level, 1 Oct 1987, 8160.

TABLE 1. SUMMARY OF TEN MEASUREMENTS FOR EACH OF FIVE SPIKELET CHARACTERS ON FOUR DIFFERENT SPECIMENS OF THE *ARISTIDA CALIFORNICA* COMPLEX. Measurements in mm. All specimens are at ARIZ.

|            | Culms pubescent         |                          | Culms glabrous          |                          |
|------------|-------------------------|--------------------------|-------------------------|--------------------------|
|            | Reeder 8238<br>AZ, YUMA | Felger 16712<br>MEX, SON | Reeder 7221<br>MEX, BCN | Wiggins 7239<br>MEX, SON |
| 1st glume  | 7.0–8.5                 | 6.5–8.0                  | 5.5–8.0                 | 7.0–9.2                  |
| 2nd glume  | 14.0–16.0               | 13.0–15.0                | 11.5–13.5               | 13.0–13.5                |
| Lemma      | 6.0–6.5                 | 5.0–6.0                  | 5.0–6.3                 | 6.2–7.0                  |
| Awn column | 11.5–16.0               | 12.0–18.0                | 12.0–16.0               | 12.0–16.0                |
| Free awn   | 35.0–40.0               | 40.0–45.0                | 22.0–27.0               | 32.0–38.0                |



TABLE 2. SUMMARY STATISTICS FOR THE FIVE KEY CHARACTERS OF THE *ARISTIDA CALIFORNICA* COMPLEX. Plants with pubescent culms (CP), n = 145; those with glabrous culms (CG), n = 84. Measurements in mm.

| Character  | Taxon | Mean  | SD    | SE    | Min. | Max. | Skewness |
|------------|-------|-------|-------|-------|------|------|----------|
| 1st glume  | CP    | 7.50  | 0.835 | 0.069 | 6.0  | 10.0 | 0.466    |
|            | CG    | 6.63  | 0.912 | 0.100 | 4.0  | 9.2  | -0.348   |
| 2nd glume  | CP    | 14.34 | 1.506 | 0.125 | 12.0 | 23.0 | 1.814    |
|            | CG    | 12.24 | 1.402 | 0.153 | 8.0  | 15.0 | -0.298   |
| Lemma      | CP    | 6.06  | 0.537 | 0.045 | 5.0  | 7.0  | 0.016    |
|            | CG    | 6.20  | 0.567 | 0.063 | 5.0  | 7.0  | -0.284   |
| Awn Col.   | CP    | 14.31 | 3.250 | 0.270 | 8.0  | 26.0 | 0.768    |
|            | CG    | 10.60 | 2.760 | 0.301 | 4.0  | 16.0 | -0.138   |
| Awn (free) | CP    | 35.12 | 5.644 | 0.469 | 25.0 | 50.0 | 0.058    |
|            | CG    | 26.07 | 6.211 | 0.678 | 13.0 | 40.0 | -0.304   |

*Aristida californica* Thurb. var. *glabrata* Vasey: USA. AZ: Cochise Co., on Willcox Rd. just E of jct. with Cascabel Rd., 975 m, 5 Jun 1987, 8041; Pima Co., Santa Rita Range Reserve along Box Canyon Rd., 1310 m, 29 May 1987, 8035; E end of Rincon Mts, 1220 m, 4 Jun 1987, 8038; Pinal Co., Pinal Pioneer Pkwy., 3 km S of Bradley Wash, 1310 m, 3 Oct 1986, 7994; Yavapai Co., along US-93, 3.5 km NW of Santa Maria River crossing, 550 m, 2 Oct 1987, 8162; along US-93, ca. 4.5 km NW of jct. with US-89, 670 m, 2 Oct 1987, 8163.

## DISCUSSION

Table 1 needs little explanation. It reveals, as we suspected, that there is a considerable amount of variation in lengths of spikelet parts on a single individual. This was taken into consideration as measurements were made on the entire suite of specimens examined in the study. For each sample numerous spikelets were measured in order to arrive at a value which seemed representative.

Perusal of Table 2 reveals that in each case there is a considerable amount of overlap in the measurements of the spikelet parts; with the lemma, this overlap is complete. With respect to glume I, we determined that 89% of CP and 88% of CG plants fell in the zone of overlap, which is 6–8 mm. Glume II had 99% of CP and 77% of CG plants in the overlap zone of 12–18 mm. The awn column showed 79% of CP and 88% of CG plants in the overlap zone of 8–16 mm. Finally, the spreading awns, with an overlap zone of 25–40 mm, revealed a similar picture: 90% of CP and 65% of CG plants fell in this zone. It is evident that lengths of these spikelet features are not good key characters to use in separating species. For each feature (except the lemma) the longest measurement is from a plant



with pubescent culms, whereas the shortest is from one in which the culms are glabrous.

#### ECOLOGY AND GEOGRAPHICAL DISTRIBUTION

The pubescent taxon occurs in southeastern California, Baja California Norte and Sur, southwestern Arizona, and in Sonora southward along coastal dunes to Bahía Colorado (south of Tastiota) and farther south from near the mouth of the Río Mayo to Topolobampo in northwestern Sinaloa (Fig. 2). This is one of the few grasses reported to be endemic to the Sonoran Desert, but, as the collections from Sinaloa indicate, it actually occurs south of the Sonoran Desert. It is also in the Mojave Desert of California.

Densely pubescent populations inhabit sandy soils, flats and dunes, in the lowland regions of the northern part of the Sonoran Desert of northwestern Sonora, extreme southwestern Arizona, southeastern California, and northeastern Baja California Norte. This area was designated by Shreve (1951) as the Lower Colorado Valley phytogeographic region of the Sonoran Desert. Here rainfall is largely winter-spring, almost entirely so in the western part, and this is also true for the Mojave Desert of southern California. There may be some summer rainfall in the more southern and eastern portion of the Lower Colorado Valley, although precipitation in this extremely arid region is unpredictable (Ezcurra and Rodriguez 1986).

The pubescent form also occurs southward into regions of relatively greater and more predictable rainfall in the Baja California peninsula and in southern Sonora and northwestern Sinaloa considerably south of Guaymas, the usually accepted boundary of the Sonoran Desert (Felger and Lowe 1976). The southern Sonora and Sinaloa populations are disjuncts, presently known from coastal dunes in the delta regions of the Río Mayo and Río Fuerte (we predict that it should also occur in coastal dunes in the delta region of the Río Yaqui). Plants from these southern populations are not as densely pubescent as are those from the Lower Colorado Valley and Mojave Desert.

*Aristida glabrata* generally occupies regions peripheral to that of *A. californica*, in areas of higher elevation (Fig. 3) and/or higher precipitation, and mostly where summer-fall rainfall is greater and more predictable. In Arizona and Sonora *A. glabrata* extends into grassland and chaparral well above the desert. In addition, this species often occurs on soils which are more rocky and gravelly than those occupied by *A. californica*. Throughout their distribution the two taxa are essentially allopatric, but in a few cases they have been collected in close proximity. Both have been found in Baja California Norte, in the San Matías Pass, at only slightly different elevations [Reeder and Reeder 7221, 700 m, *A. glabrata* (ARIZ); and Thorne



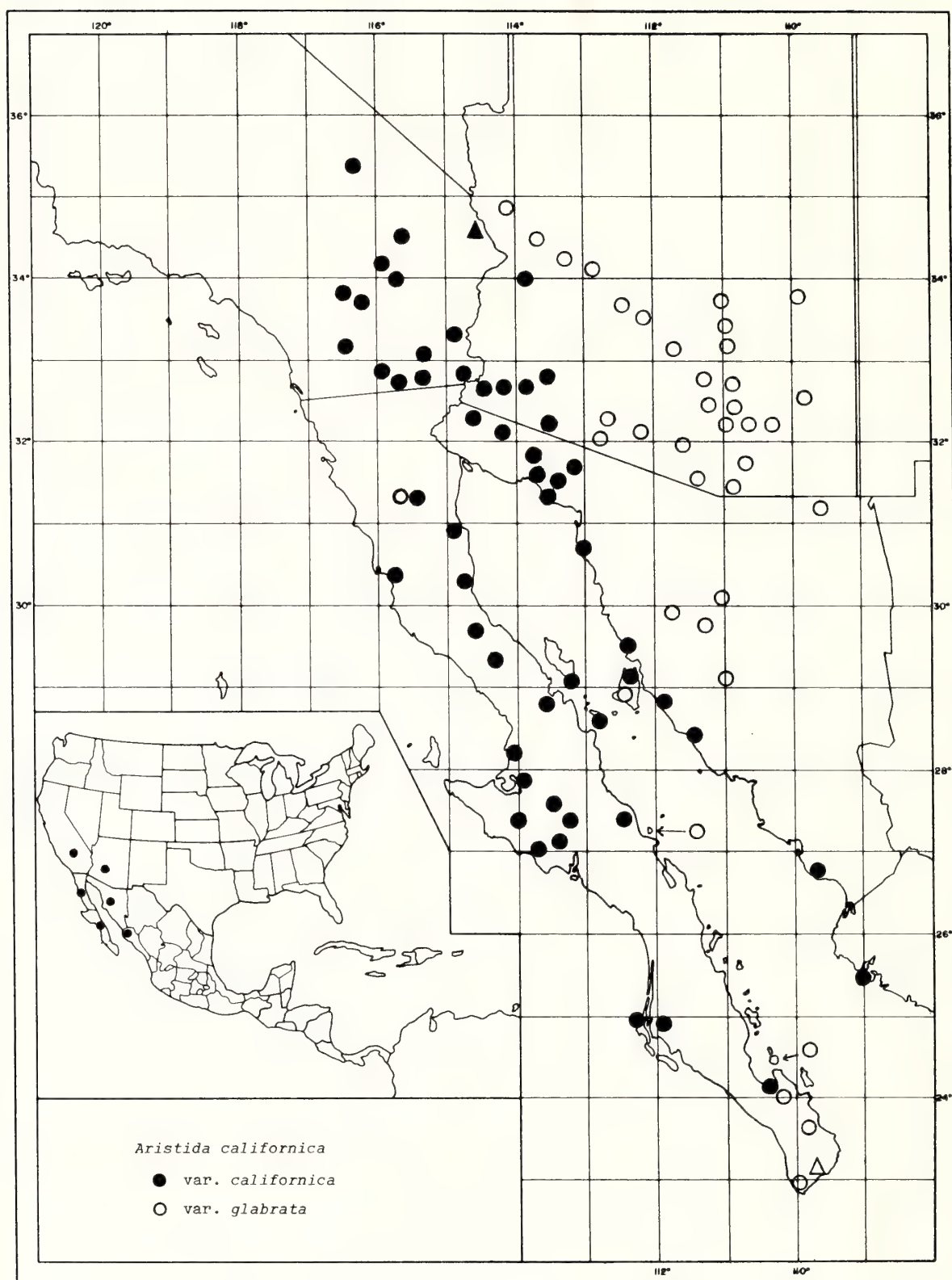


FIG. 2. Map showing the range for the two varieties of *Aristida californica*: *var. californica* (solid circles); *var. glabrata* (open circles). Triangles represent type localities.

and Charlton 60184, 600 m, *A. californica* (RSA)]. Another somewhat similar situation is encountered in the vicinity of La Paz, Baja California Sur. There are several collections of *A. glabrata* from that region, and we have seen one gathering of *A. californica* from this



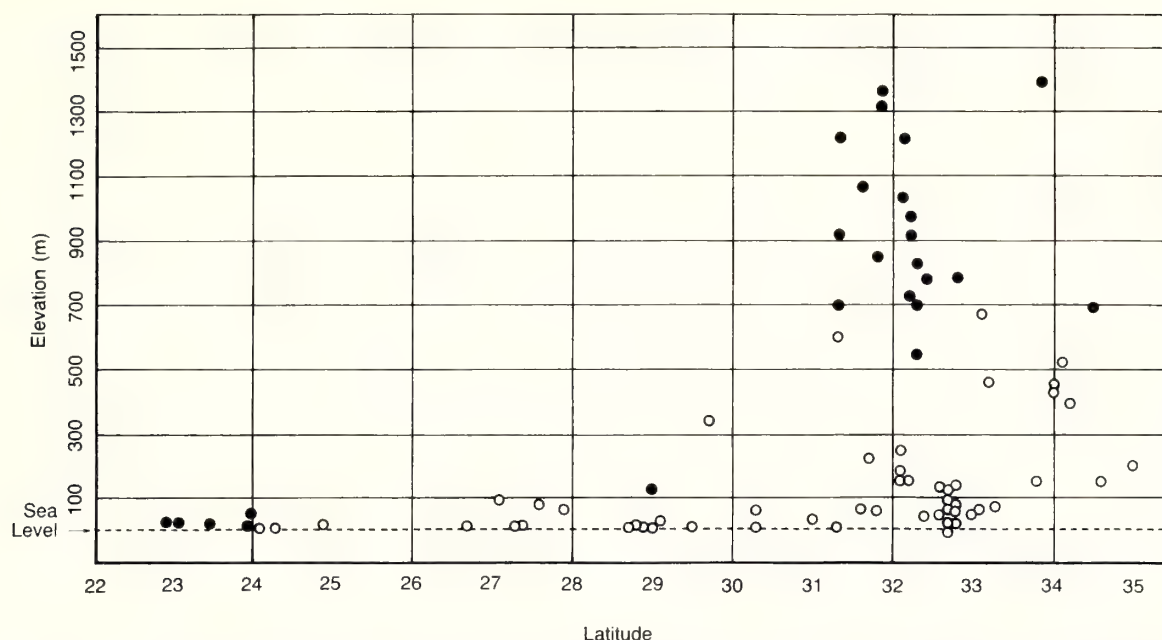


FIG. 3. Elevational distribution for *Aristida californica* var. *californica* (solid circles) and var. *glabrata* (open circles).

same area [Carter 2726 (UC)]. Both taxa have also been found on Tiburón Island in the Gulf of California. *Aristida californica* [Felger and Russell 7009; Felger et al. 12537 (ARIZ)] is common on the beach dunes of the arid eastern and northern coasts (Felger and Lowe 1976); one collection of *A. glabrata* [Felger et al. 17351 (ARIZ)] was made from the large interior central valley, a considerable distance inland, at an elevation of 120 m. The interior of this large island supports a much denser, less xerophytic vegetation and undoubtedly has higher rainfall than does the arid coast (Felger 1966; Felger and Lowe 1976). A noteworthy gathering of *A. glabrata* is Wiggins 17335 (RSA) from Isla San Marcos, situated near the eastern coast of Baja California Sur slightly south of Santa Rosalia. All collections of this complex on the Baja California peninsula between the San Pedro Mártir in the north and La Paz in the south have pubescent culms (*A. californica*).

Within the Pinacate Region and Gran Desierto of northwestern Sonora, one sees a trend of more densely pubescent plants in more xeric habitats. Populations farther inland in the Gran Desierto tend to have stems more densely white-pubescent than those growing under the more equable conditions along the coast.

It seems apparent, therefore, that the distribution of pubescent and non-pubescent forms correlates with vegetational and ecological factors. *Aristida glabrata* occupies regions of more predictable and higher precipitation, especially summer-fall rainfall, and is replaced by *A. californica* in hotter, drier climates with cool season rains. Presuming the Sonoran Desert to be more recent than thornscrub, one may speculate that the origin of pubescent forms pre-dates the Sonoran Desert. Such plants may have evolved as coastal dune-



adapted plants along the great river deltas of subtropical scrub regions of northwestern Sinaloa and southwestern Sonora.

#### SUMMARY

The two taxa, *Aristida californica* and *A. glabrata*, are clearly closely related, and have the same chromosome number ( $2n=22$ ). Vegetatively they are very similar, with essentially the same growth habit. Measurements of the spikelet parts show a high degree of overlap, which is complete with respect to the lemma. Nevertheless, the measurements are skewed; the longest for each character (except the lemma) was always found on plants with pubescent culms. Even though their geographical ranges are reasonably separate, and they tend to occur at different elevations, we conclude that it is more realistic to treat them as varieties of a single species. Some might prefer to designate them as subspecies, but we make no distinction between subspecies and variety when only one infraspecific level is recognized.

#### ACKNOWLEDGMENTS

We are indebted to the curators at ASU, CAS-DS, RSA-POM, SD, and UC-JEPS for the loan of herbarium specimens. Grateful appreciation is also extended to Janice Bowers and Tony Burgess for assistance in computer mapping; to J. Mark Porter and L. J. Toolin for helpful discussions; to Charlotte Reeder for assistance with the literature and critically reading the manuscript; and to C. T. Mason, Jr., for providing space at ARIZ and arranging for loans from other herbaria.

#### LITERATURE CITED

- EZCURRA, E. and V. RODRIGUEZ. 1986. Rainfall patterns in the Gran Desierto, Sonora, Mexico. *J. Arid Environ.* 10:13–28.
- FELGER, R. S. 1966. Ecology of the gulf coast and islands of Sonora, Mexico. Ph.D. dissertation. Univ. Arizona. 570 pp.
- FELGER, R. S. and C. H. LOWE. 1976. The island and coastal vegetation and flora of the northern part of the Gulf of California. *Los Angeles County Mus. Contr. Sci.* 285. 59 pp.
- GOULD, F. W. and R. MORAN. 1981. The grasses of Baja California, Mexico. *Mem. San Diego Soc. Nat. Hist.* 12. 140 pp.
- HENRARD, J. T. 1926. A critical revision of the genus *Aristida* being a preliminary study and an introduction to the Monograph, vol. 1. *Meded. Rijks Herb.* No. 54, Leiden. VIII + 220 pp.
- HITCHCOCK, A. S. 1924. The North American species of *Aristida*. *Contr. U.S. Natl. Herb.* 22:517–586 + index.
- . 1951. Manual of the grasses of the United States. (Ed. 2, revised by A. Chase.) U.S. Dept. Agric. Misc. Publ. 200. 1051 pp.
- NUTTALL, T. 1818. The genera of North American plants, and a catalogue of the species, to the year 1817. Printed for the author by D. Heartt, Philadelphia. Vol. 1, viii + 312; Vol. 2, 254 pp. + index and erratum, additions.
- PALISOT DE BEAUVOIS, A. M. F. J. 1812. *Essai d'une nouvelle Agrostographie; ou nouveaux genres des Graminées.* Paris. lxxiv + 182 pp. + xxv plates.
- REICHENBACH, H. G. L. 1828. *Conspectus Regni Vegetabilis per Gradus Naturales Evoluti.* xiv + 294 pp. Lipsiae.



- SHREVE, F. 1951. Vegetation of the Sonoran Desert. Publ. Carnegie Inst. Washington 591:i-xii, 1-192. Reprinted in F. Shreve and I. L. Wiggins, Vegetation and Flora of the Sonoran Desert. Stanford Univ. Press. 1964.
- THURBER, G. 1880. Gramineae. Pp. 253-328 in S. Watson, Botany [of California] vol. 2. John Wilson and Son, Boston.
- TRINIUS, C. B. and F. J. RUPRECHT. 1842. Gramina Agrostidea. III. Callus obconicus (Stipacea). Mém. Acad. Imp. Sci. St.-Petersbourg Sér. 6, Sci. Nat. 7(2):1-189. [1843]. Preprinted as Species Graminum Stipaceorum (1842).
- VASEY, G. 1891. Gramineae. Pp. 177-179 in T. S. Brandegee, Flora of the Cape Region of Baja California. Proc. Calif. Acad. Sci. II. 3:108-182.

(Received 12 Jan 1989; revision accepted 11 May 1989.)

## ANNOUNCEMENT

### THE 1989 JESSE M. GREENMAN AWARD

The 1989 Jesse M. Greenman Award has been won by Carol A. Todzia for her publication "Chloranthaceae: *Hedyosmum*," which appeared in Flora Neotropica Monographs, volume 48. This monograph is derived from a Ph.D. dissertation submitted to the University of Texas, under the direction of Dr. Beryl B. Simpson. The genus *Hedyosmum* is comprised of 40 species of predominantly montane, neotropical shrubs and trees. The comprehensive monograph, which includes four newly described species, reexamines previous treatments of the genus and presents new data on anatomy, morphology, ecology, and geography. Synopses of the taxonomic history, palynology, cytology, and uses are also provided.

This Award is named for Jesse More Greenman (1867-1951), who was Curator of the Missouri Botanical Garden Herbarium from 1919 until 1943. A cash prize of \$500 is presented each year by the Garden, recognizing the paper judged best in vascular plant or bryophyte systematics based on a doctoral dissertation published during the previous year.

Nominations for papers published during 1989 are now being accepted for the 22nd annual award, which will be presented in the summer of 1990. Reprints of such papers should be sent to: Greenman Award Committee, Research Division, Missouri Botanical Garden, P.O. Box 299, St. Louis, MO 63166-0299, U.S.A. In order to be considered for the 1990 award, reprints must be received by 1 June 1990.



# A NEW SPECIES OF *SIPHONOGLOSSA* (ACANTHACEAE) AND SOME INFRAGENERIC TRANSFERS

RICHARD A. HILSENBECK<sup>1</sup>

Department of Botany, The University of Texas at Austin,  
Austin, TX

## ABSTRACT

*Siphonoglossa mexicana* (Acanthaceae), a new species from Mexico, is described and illustrated. The new species is most closely related to *S. ramosa* and *S. canbyi* of *Siphonoglossa* sect. *Siphonoglossa*. Characters, variation patterns, and reproductive biology of the species are discussed with direct reference to an earlier treatment that combined *S. ramosa*, *S. discolor*, and *S. hondurensis* under the name *S. sessilis*. *Siphonoglossa ramosa* and *S. sessilis* are retained as distinct species, and the new combinations, *S. ramosa* var. *discolor* and *S. ramosa* var. *hondurensis*, are proposed. Additionally, *S. calcarea* of northern Colombia is reduced to a variety of *S. sessilis*.

## RESUMEN

*Siphonoglossa mexicana* Acanthaceae, una nueva especie de Mexico, es descrita y ilustrada. La nueva especie parece estar mas relacionada a *S. ramosa* y *S. canbyi* de *Siphonoglossa* seccion *Siphonoglossa*. Caracteres, modelos de variacion y biologia reproductiva de la especie son discutidas con referencia a un tratamiento anterior que combina *S. ramosa*, *S. discolor* y *S. hondurensis* bajo el nombre *S. sessilis*. *Siphonoglossa ramosa* y *S. sessilis* se mantienen como especies distintas, y las nuevas combinaciones, *S. ramosa* var. *discolor* y *S. ramosa* var. *hondurensis*, son propuestas. Adicionalmente, *S. calcarea* de el norte de Colombia se reduce a variedad de *S. sessilis*.

In connection with a monographic treatment and chemosystematic investigation of the genus *Siphonoglossa* Oerst. (Acanthaceae), I have discovered several new taxa. Two of these new species, *S. durangensis* (sect. *Siphonoglossa*) and *S. linearifolia* (sect. *Pentaloba*) were previously described by Henrickson and Hilsenbeck (1979). A third new species is proposed here.

***Siphonoglossa mexicana* Hilsenbeck, sp. nov.** (Fig. 1). — TYPE: MEXICO, Sinaloa, Imala, shady wooded ravine in valley, 500 ft, 29 Nov 1939, H. S. Gentry 5099 (holotype, CAS; isotypes, GH, MO, NY, US).

A speciebus affinibus caulibus saepe brunneis, pilis caulium confertis brevibus uniformibus 0.1–0.3 mm longis; foliis tenuibus mem-

<sup>1</sup> Present address: Department of Biology, Sul Ross State University, Alpine, TX 79832.



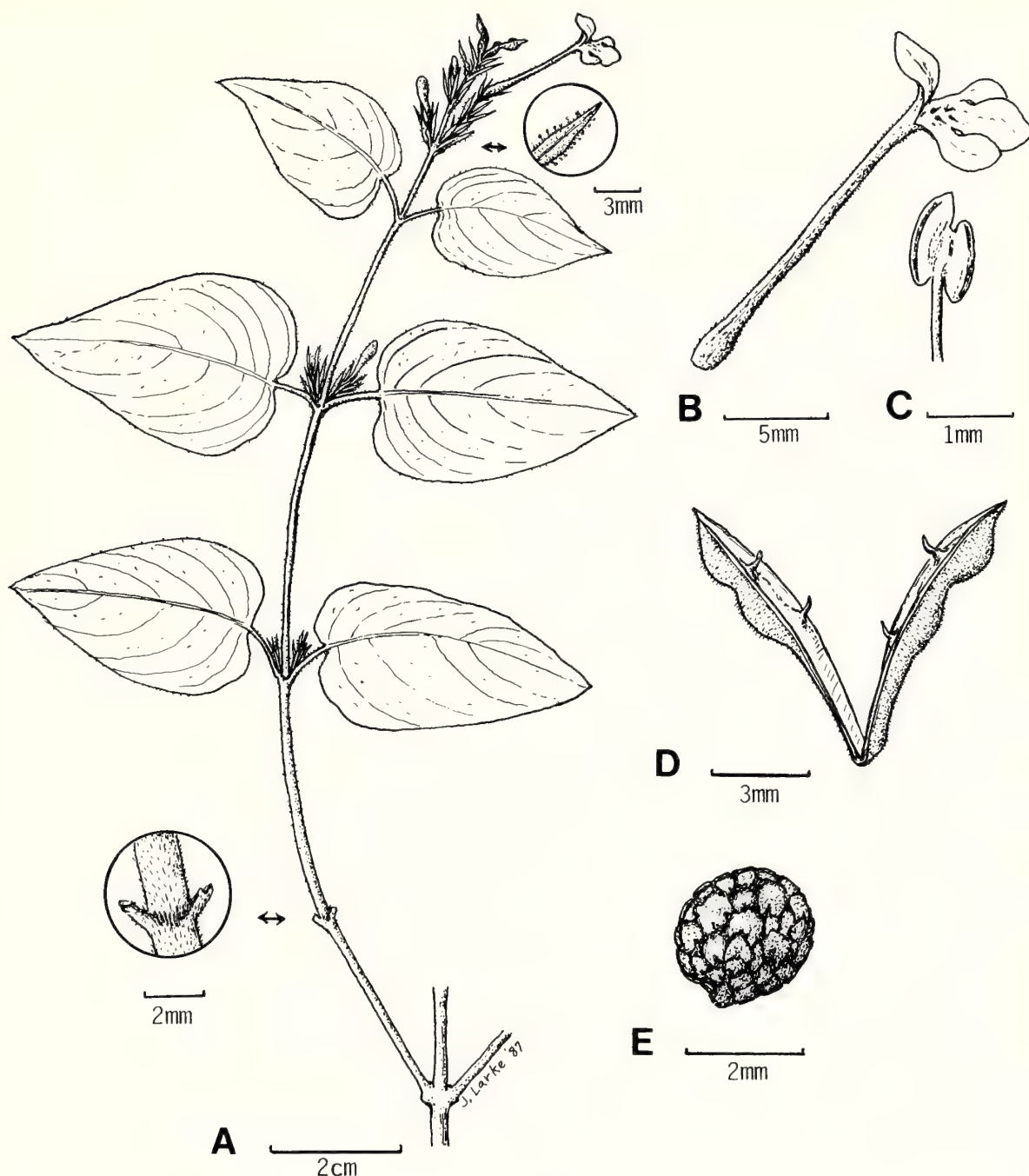


FIG. 1. *Siphonoglossa mexicana* Hilsenbeck. A. Branch showing flowering spikes and detail of stem and bract pubescence. B. Corolla showing characteristic long tube and "crowfoot" pattern on anterior lip. C. Anther, posterior view. D. Open fruit showing retinacula. E. Seeds showing characteristic muricate encrustations of the testa.

branaceis; floribus oppositis (raro alternis) in spicis dispositis, bracteis (3.5–)4–6 mm longis hispidis trichomatibus pro parte simplicibus pro parte glandularibus confertis sparsisve; fructis 7–9(–11) mm longis; seminibus ca.  $2 \times 2$  mm, testis incrustedis incrustationibus imbricatis proximaliter acutis (0.2–)0.3–0.4 mm latis differt.

Erect, ascending or clambering perennial herb to subshrub, branched above, (3–)5–10 dm high, from a rhizomatous rootstock;



stems terete, striate, greenish to brownish above, covered with a short, even pubescence of erect to recurved hairs 0.1–0.2(–0.3) mm long, usually dark brown and becoming woody below. Leaf blades thin, membranaceous, lance-ovate to ovate, (2.5–)4–6(–7.5) cm long, (1.5–)2–3.5(–4) cm wide; tip acute to long acuminate; base often slightly oblique becoming attenuate to a petiole (4–)8–10(–15) mm long; margin entire to slightly repand with hairs to 0.5 mm, olive green above, paler and duller beneath, densely lineolate, nearly glabrous above except along veins with scattered hairs to 0.2 mm, hispid beneath with scattered hairs 0.4–0.7 mm long. Inflorescence of narrow terminal and axillary spikes; flowers usually opposite, nearly sessile; bracts linear lanceolate, (2.5–)4–6 mm long, 0.6–1 mm wide at base, hispid with mixed simple and glandular trichomes; bracteoles linear to subulate, 3–3.5 mm long, hispid. Calyx deeply 4-parted, 4.5–5.5 mm long; segments lanceolate 4–5 mm long (occasionally with a greatly reduced fifth posterior segment to 1 mm long), hispid and usually densely covered with glandular trichomes. Corolla pink to pale purple, zygomorphic, (19–)22–28 mm long; posterior lip entire, erect to slightly recurved, 4.5–6 mm long, 1.5–2 mm wide; anterior lip 3-lobed, spreading, the middle lobe 5.5–8 mm long, 2.5–4 mm wide with a purple to reddish "crow-foot" pattern on the wrinkled palate at the narrow throat, the lateral lobes 5–7 mm long, 2–3.5 mm wide; tube (13–)15–20 mm long, terete, pubescent with scattered hairs on exterior surface. Style 16–23 mm long, slightly exserted from beneath posterior lip; stigma linear, posterior lobe greatly reduced. Stamens 2, barely exserted; filaments 2.5–3.5 mm long, inserted near base of lateral lobes; anthers 2-celled, 1.2–1.5 mm long, the anther sacs slightly superposed and oblique, the upper sac 1.1–1.2 mm long, the lower sac 0.9–1 mm long, the bases blunt; connective 0.3–0.4 mm wide. Fruit a clavate, medially constricted capsule with elliptic head, 7–9(–12) mm long, with the base a solid stripe 2–4 mm long, light brown or tan, often glandular pubescent; seeds 4, (1.8–)2 × 2(–2.2) mm, light yellowish-tan prior to maturity, dark brown when mature, muricate, the irregular and pointed encrustations (0.2–)0.3–0.4 mm in diameter, forming somewhat overlapping plates. Chromosome number  $n=11$  (*Hilsenbeck* 790, 797).

PARATYPES: MEXICO, Guerrero, Distr. Mina, Puerto de Oro, 500 m, 9 Nov 1936, *Hinton* 9831 (GH, K, LL, MICH, TEX); 1 km al N de Xalitla, 740 m, 18 Nov 1975, *Lopez H. s.n.* (ENCB). Jalisco, ca. 5 mi N of Tomatlan, ca. 200 ft, 17 Mar 1982, *Daniel* 2079 (TEX). Morelos, Pedregal de Cuernavaca, 24 Dec 1960, *Paray* 3137 (ENCB); cañon de Lobos, 1270 m, 4 Dec 1970, *Vazquez* 2782 (MEXU). Puebla, ca. 8 mi SE of Izucar de Matamoros on Mexico Hwy 190, 1100 m, 24 Nov 1980, *Hilsenbeck* 797 (TEX); 2 km SE de Petlan-cingo, sobre la carretera a Huajuapán, 1450 m, 29 Nov 1972, *J.*



*Rzedowski 28928* (ENCB); ca. 20 km SE of Izucar de Matamoros, 1150 m, 18 Feb 1965, *McVaugh 22485* (ENCB, MICH). Veracruz, ca. 4 km off Mexico Hwy 140, E of Palo Gacho, on rd to Actopan, ca. 200 m, 22 Nov 1980, *Hilsenbeck 790* (TEX); Actopan, 150 m, 5 Nov 1970, *Ventura A. 2761* (ENCB); Plan del Río, 300 m, 10 Sep 1974, *Ventura A. 10510* (ENCB); Sinaloa, Ymala, 25 Sep–8 Oct 1891, *Palmer 1712* (US). No locality (but probably Guerrero), 1791, *Haenke 988* (F).

*Siphonoglossa mexicana* has a 4-parted calyx, flowers disposed in spikes with subulate bracts and bracteoles, an entire posterior corolla lip, blunt anther sacs, and ellipsoidal capsule heads. These features characterize sect. *Siphonoglossa* and, therefore, this species clearly belongs in the type section. The new species is related most closely to two other Mexican species: *S. ramosa* Oersted, the type species of the genus found primarily in Puebla and Oaxaca of southern Mexico, and *S. canbyi* (Greenman) Hilsenbeck of Tamaulipas and Nuevo Leon in northeastern Mexico. *Siphonoglossa mexicana* has been misidentified consistently as *S. ramosa* or *S. canbyi*. Because *Siphonoglossa* had never been monographed and no keys have been written, uncertainty as to what characters delimited these species has existed until now (Table 1).

*Siphonoglossa mexicana* is the most widespread species of the genus in Mexico. It extends from the state of Veracruz on the Gulf Coast westward across the northern edge of the Isthmus of Tehuantepec and then northward through Guerrero and Michoacán to Sinaloa. This species is somewhat variable throughout its range and is therefore difficult to accurately identify, but can be distinguished from other taxa of *Siphonoglossa* by the combination of: 1) thin, membranaceous, often long-petiolate leaves; 2) flowers opposite on the spikes with bracts mostly 4.5–6 mm long; 3) bracts and calyx hispid pubescent often with a dense covering of glandular trichomes; 4) usually smaller (7–9 mm) fruit; and 5) seeds with muricate, overlapping encrustations (0.2–)0.3–0.4 mm wide. In some populations of *S. mexicana*, the flowers become somewhat alternately arranged in the spike and the glandular trichomes on the inflorescence become sparse, but the other characters cited serve to distinguish this species.

Additional morphological (Hilsenbeck 1983) and chemical data (Hilsenbeck unpubl.), as well as recent collections primarily from western Mexico (Daniel pers. comm.), strongly suggest that *S. mexicana* intergrades with *S. ramosa* var. *ramosa* in Oaxaca and Puebla. Furthermore, these same data suggest that *S. mexicana* also intergrades extensively with *S. canbyi* in southern Veracruz and across the northern Isthmus of Tehuantepec into Guerrero with some populations of *S. mexicana* even as far north as Sinaloa exhibiting variation in pubescence, bracts, capsule, and seed morphology in the direction of *S. canbyi*. The significance and extent of this vari-



TABLE 1. MORPHOLOGICAL DIFFERENCES BETWEEN *SIPHONOGLOSSA MEXICANA*, *S. RAMOSA*, AND *S. CANBYI*

|                    | <i>S. mexicana</i>                                    | <i>S. ramosa</i>  | <i>S. canbyi</i>                               |
|--------------------|---|---|--|
| Stem pubescence    | short, mostly even and erect, 0.1–0.2 mm long         | usually recurved to spreading, 0.5–1.2 mm long            | 2 decussating lines, recurved, 0.4–0.6 mm long |
| Petiole            | mostly 8–10 mm long                                   | 2–5 mm long   | 3–7 mm long                                    |
| Leaf texture       | thin, membranaceous                                   | chartaceous   | thick, coriaceous                              |
| Flower arrangement | mostly opposite                                       | opposite  | alternate                                      |
| Bracts             | (2.5–)4–6 mm long                                     | 2–3(–4) mm long   | 1.5–2.5 mm long                                |
| Bract pubescence   | hispid, mostly with dense glandular trichomes         | densely pilose-hispid rarely with few glandular trichomes | glabrous to sparingly hirsute                  |
| Fruit              | 7–9 mm long (up to 12 mm in introgressed populations) | 9–11 mm long  | 10–14 mm long                                  |
| Seed coat          | muricate encrustations, 0.2–0.4 mm in diameter        | muricate encrustations, 0.3–0.5 mm in diameter            | papillose tubercles, 0.2 mm in diameter        |



ation pattern are discussed more fully in an upcoming monograph of the genus and by Hilsenbeck (1983). It is clear, however, that *S. mexicana* is a good species, albeit one that may hybridize along the southern and eastern edges of its range, but one that accounts for most of the variation within the genus in western Mexico.

#### NEW COMBINATIONS

Because I recognize *S. ramosa* and *S. sessilis* as distinct species (Hilsenbeck 1983), it is necessary to address the treatment of the genus for the Flora of Guatemala (Gibson 1972, 1974). Gibson (1972) combined the type species, *S. ramosa*, with *S. discolor* S. F. Blake and *S. hondurensis* Standley & Steyerf., under the name *S. sessilis* (Jacq.) D. Gibson. Radlkofer (1883), however, had previously made the combination, as suggested by Oersted, and, thus, the proper citation of the name of this species is *S. sessilis* (Jacq.) Oersted ex Radlk. Furthermore, by not examining the type material of *S. ramosa* and merging this species with *S. sessilis* apparently on the basis of Oersted's original description of *S. ramosa*, Gibson overlooked the first of two consistent and discontinuous characters which separate *S. ramosa* and *S. sessilis*. Oersted (1854) states that the flowers of *S. ramosa* are solitary and sessile in the leaf axils, but in the type material of *S. ramosa* a spike is clearly evident.

I have observed, both in natural populations (including one near the type locality) and in greenhouse cultures of *S. ramosa*, that only the first few flowers are solitary in the leaf axils, but later flowers are always in spikes. On the other hand, populations of *S. sessilis*, observed in full flower in the field (Dominican Republic) and in the greenhouse, as well as all herbarium sheets of this species that I have examined, never produce a spike; the flowers are always solitary and sessile in the leaf axils. This is a conspicuous and consistent difference between the two species.

A second major difference between the two taxa is the type of seed coat sculpturing. In *S. ramosa*, the seed coat has large (0.3–0.5 mm), partially overlapping, bullate encrustations that are often muricate at their proximal ends (as in *S. mexicana*, Fig. 1, H). The seed coat of *S. sessilis*, although basically similar, has tuberculate or papillose protuberances that are always much smaller (0.1 rarely to 0.2 mm in diameter), discrete and not overlapping, and rounded, not pointed or sharp. Because these differences are consistent across the ranges of the two species, I feel the two taxa should be maintained as species.

These same two characters further disclose a very close morphological relationship between *S. ramosa* and two taxa distributed well to the south (i.e., Central America) of its range. Both *S. discolor* and *S. hondurensis*, which Gibson also placed in *S. sessilis*, have the seed coat morphology characteristic of *S. ramosa*, whereas the other



species of the genus (except *S. mexicana*) have the seed coat morphology characteristic of *S. sessilis*. In addition, *S. hondurensis* consistently produces its flowers in spikes. The only collection of *S. discolor* is represented by a holotype and an isotype of which the few available flowers are solitary and sessile in the axils. One might be tempted, therefore, to place this taxon within *S. sessilis*, if seed morphology were not considered. It is apparent from the lack of flowers and/or fruits that the material of *S. discolor* was collected at the beginning of the flowering season and, thus, it is likely that this population, although perhaps genetically capable of producing flowering spikes, was collected before any definite spikes could be produced. Unfortunately, no observations of *S. discolor* in the field or greenhouse have been conducted. In the isotype, however, the beginnings of what appears to be a spike can be seen. Because of these morphologic similarities between *S. ramosa* and *S. discolor*, I propose the following combination.

*Siphonoglossa ramosa* Oersted var. *discolor* (S. F. Blake) Hilsenbeck, comb. nov.—*Siphonoglossa discolor* S. F. Blake, Contr. U.S. Natl. Herb. 24:25. 1922.—TYPE: GUATEMALA. Zacapa, edge of thicket at Gualan, 26 May 1919, *S. F. Blake* 7669 (holotype, US!; isotypes, GH!, fragment F!).

This variety is known only from the type collection. The label on the types states that the specimens were collected in the Department of Izabel, but in the description Blake (1922) states that the collection was made in the Department of Zacapa. This variety may be recognized by a combination of the strongly discolorate leaves with cuneate bases and usually prominent apiculate tips and the very fine (0.1 mm) even stem pubescence.

The type specimen, and all other collections of *S. hondurensis*, have their flowers disposed in spikes. In their description of *S. hondurensis*, Standley and Steyermark (1952) state that this species differs from *S. discolor*, the only other species in Central America, in its foliage and details of the inflorescence. These differences, however, do not hold when the total variation of the taxa is considered and are not of sufficient magnitude to warrant the retention of *S. hondurensis* as a species. It shares with *S. ramosa* spikes with opposite flowers and short bracts, bracteoles and calyx with hirsute-hispid pubescence, and characters of the seed coat. I feel it is best to place *S. hondurensis* at the varietal level, thus recognizing its populational variation and slight divergence from *S. ramosa* var. *ramosa* of Puebla and Oaxaca, rather than to synonymize it with *S. ramosa* and obscure its variation pattern. I therefore propose the following new combination.



*Siphonoglossa ramosa* Oersted var. *hondurensis* (Standley & Steyererm.) Hilsenbeck, comb. nov.—*Siphonoglossa hondurensis* Standl. & Steyererm., Ceiba 3:131. 1952.—TYPE: H. Morazán: moist thicket, vicinity of Suyapa, region of La Travesia, 1100–1200 m, 18 Sep 1948, *P. C. Standley 12459* (holotype, F!).

*Additional specimens examined:* COSTA RICA, Guanacaste, near Cataract Falls, Hacienda Tenorio, 16 Feb 1956, *Schubert 1066* (US). GUATEMALA, Jutiapa, vicinity of Jutiapa, ca. 850 m, 24 Oct–5 Nov 1940, *Standley 75836* (F); between Jutiapa and La Calera, SE of Jutiapa, ca. 850 m, 2 Nov 1940, *Standley 76098* (F). HONDURAS, Comayagua, near Agua Salada, 650 m, 29 Sep–5 Oct 1951, *Williams 18320* (F); Morazán: vicinity of Suyapa, region of La Travesia, 1100–1200 m, Sep–Dec, *Standley 12453* (F); near San Francisco, 800 m, 21 Aug 1949, *Standley 22988* (F, NY); along Río Yeguaré near San Francisco, 850 m, 21 Aug 1949, *Williams 15912* (F); along Río Yeguaré, E of El Zamorano, 850 m, 10 and 15 Dec 1946, *P. C. Standley 1090* (F); near El Jicarito along road toward El Pedregal, ca. 900 m, 6 Ju 1949, *Standley 20845* (F); mountains above El Jicarito, near Río Caparrosa, 900–1300 m, 26 May 1951, *Standley 28492* (F); Margenes de la Quebrada de las Burras entre Suyapa y Tegucigalpa, 1050 m, 11 Dec 1948, *Molina R. 1836* (F, GH); vicinity of Suyapa, 1100–1200 m, Sep–Dec 1948, *Standley 15394* (F); Dpto. de Francisco, Morazan, 1 Aug 1975, *Garcia 104* (MO); Olancho: vicinity of Catacamas, 450–500 m, 18–26 Mar 1949, *Standley 18432* (F); vicinity of Catacamas, 450–500 m, 18–26 Mar 1949, *Standley 18408* (F).

Variety *hondurensis* may be distinguished from var. *ramosa* by a combination of the dark brown stems, the more ovately-lanceolate leaves, and the usually shorter corollas. In the holotype, an inflorescence is not readily apparent, but the beginning (or vestige?) of a spike can be seen at two places on the specimen. Almost all of the other specimens seen have several conspicuous flowering spikes.

Leonard (1958) described *Siphonoglossa calcarea* based on a single collection from La Paz, Department of Magdalena, in extreme northeastern Colombia. This taxon is clearly conspecific with *S. sessilis*; almost every qualitative and quantitative character of *S. calcarea* falls within the range of variation of *S. sessilis*. These two taxa share a similar seed coat morphology, and in both the flowers are always solitary in the leaf axils. *Siphonoglossa calcarea* differs from *S. sessilis* by its reduced stature and its hirtellous stem pubescence, minor character differences which may have been environmentally induced by the "very dry limestone soil" from which the type specimen was collected. So similar are these two taxa, that I have some reservations in recognizing, at any rank, the material from La Paz. Because there



are slight differences between the two taxa, however, and because *S. calcarea* is outside the known range of *S. sessilis*, I choose to recognize it at the varietal level. By doing so, I hope that the variation of this population will be brought to the attention of botanists and further collections will be encouraged.

*Siphonoglossa sessilis* (Jacq.) Oersted ex Radlk. var. *calcarea* (Leonard) Hilsenbeck, comb. nov.—*Siphonoglossa calcarea* Leonard, Contr. U.S. Natl. Herb. 31:402. 1958.—TYPE: COLOMBIA, Magdalena, on very dry limestone soil at La Paz, 200 m, 14 Jan 1944, O. Haught 3929 (holotype, US!).

*Siphonoglossa sessilis* var. *sessilis* may be distinguished readily from other taxa of *Siphonoglossa* by a combination of the solitary (rarely 2), sessile or very short-peduncled, axillary flowers, the nearly glabrous short bracteoles (1.5–3 mm) and sepals (2.5–3.5 mm), and the nearly glabrous fruits which are 8–10 mm long. *Siphonoglossa sessilis* var. *calcarea* may be distinguished from the typical variety by a combination of the densely hirtellous stems, petioles and bractlets, and the somewhat shorter (7–8 mm long), densely hirtellous capsules. The single collection that represents the holotype is the only known material of this variety.

How Leonard overlooked the similarities between *S. calcarea* and *S. sessilis* may be explained partially by his belief that *S. sessilis* belonged to *Justicia*. Thus, he may have never considered the two taxa in the same light. Leonard (1958) placed *Siphonoglossa* in the Odontonemeae, where Lindau (1894, 1895) had placed it. Henrickson and Hilsenbeck (1979) and Hilsenbeck (1979), however, have shown that *Siphonoglossa* belongs in the Justicieae. The generic concept of *Siphonoglossa* and its circumscription relative to *Justicia* will be discussed in a future paper dealing with generic concepts and delimitation in the Justicieae.

#### ACKNOWLEDGMENTS

I sincerely thank James Henrickson and Tom F. Daniel for helpful discussions and encouragement, and Daniel for providing collections of the new species from Jalisco and Michoacán, Mexico, where it was previously unknown. I also thank Marshall C. Johnston for the Latin translation of the diagnosis, Julia Larke for the preparation of the illustration, and Jacquelyn Kallunki for editorial assistance. This study was partially supported by the National Science Foundation, Grant DEB 8014249.

#### LITERATURE CITED

- BLAKE, S. F. 1922. New plants from Guatemala and Honduras. Contr. U.S. Natl. Herb. 24:1–32.  
GIBSON, D. N. 1972. Studies in American plants (Guatemala). Fieldiana Bot. 34: 57–87.  
———. 1974. Acanthaceae. In P. C. Standley, L. O. Williams, and D. N. Gibson (eds.), Flora of Guatemala. Fieldiana Bot. 24 X, nos. 3, 4:438–461.



- HILSENBECK, R. A. 1979. Tribal and subtribal realignment of *Siphonoglossa* (Acanthaceae). Abstract Bot. Soc. Amer. Misc. Publ. 157:59.
- . 1983. Systematic studies of the genus *Siphonoglossa sensu lato* (Acanthaceae). Ph.D. dissertation. Univ. Texas, Austin.
- HENRICKSON, J. and R. A. HILSENBECK. 1979. New taxa and combinations in *Siphonoglossa* (Acanthaceae). Brittonia 31:373–378.
- LEONARD, E. C. 1958. The Acanthaceae of Colombia. Contr. U.S. Natl. Herb. 31: 1–781.
- LINDAU, G. 1894. Beiträge zur Systematik der Acanthaceen. Bot. Jahrb. 18:36–64.
- . 1895. Acanthaceae. In A. Engler (ed.), Die Naturlichen Pflanzenfamilien 4, 3b:274–354.
- OERSTED, A. S. 1854. Mexico og Centralamerikas Acanthaceer. Vidensk. Medd. Naturl. For. Kjobenhavn. 6:113–181.
- RADLKOFER, L. 1883. Ueber den systematischen Werth der Pollenbeschaffenheit bei den Acanthaceen. Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München II. 13:256–314.
- STANDLEY, P. C. and J. STEYERMARK. 1952. In P. C. Standley and L. O. Williams, Plantae Centrali-Americanae, IV. Ceiba 3:101–132.

(Resubmitted 6 Dec 1988; revision accepted 10 May 1989.)

## NOTEWORTHY COLLECTIONS

### CALIFORNIA

*POLYGONUM MARINENSE* Martens and Raven (POLYGONACEAE).—Marin Co., Escalle Marsh, ca. 150 m SE of Bon Air Bridge along the SW shore of Corte Madera Creek, T1N R6W sect. 16, NE ¼, in salt marsh with *Distichlis spicata* and *Salicornia virginica*, 15 Jun 1987, *Schierenbeck s.n.* (JEPS). Two populations of about 20 and 25 plants, respectively. Both populations ca. 8 m from the shoreline edge of vegetation. Identification confirmed by J. Hickman.

*Significance.* Rediscovery of population last seen 23 April 1944 by J. Howell, previously thought to have been extirpated. One of two known extant occurrences. This population is threatened by housing development. The other population on Pt. Reyes near the end of Schooner Bay just north of Sir Francis Drake Highway was not found during the last visit in 1984 by R. Fowler.—KRISTINA A. SCHIERENBECK, Department of Botany, Washington State University, Pullman, WA 99164-4230.

### OREGON

*PANICUM RIGIDULUM* Bosc ex Nees (Poaceae).—Douglas Co., Umpqua River, 7 mi [11.3 km] S of Elkton, T23S R7W sect. 30, 40 m, 20 Sep 1988, *Zika 10635* (OSC). Growing with *Leersia oryzoides*, *Eleocharis acicularis*, and *E. palustris* in damp ground on the east riverbank.

*Significance.* First record for Oregon. Previous West Coast reports from California and British Columbia; native from the Great Lakes to the Atlantic, where it is commonly associated with the same taxa.

*P. rigidulum* has long been known as *P. agrostoides* Sprengel, an illegitimate name (Voss, Rhodora 68:435–463, 1966). Recent eastern authors (Dore and McNeill, 1980, Grasses of Ontario, Mitchell, 1986, A Checklist of New York State Plants, Kartesz and Kartesz, 1980, A Synonymized Checklist of the Vascular Flora of the United States, Canada, and Greenland, agree that the author of *P. rigidulum* is Bosc ex Nees, and do not recognize the former Fernaldian varieties of *P. agrostoides*.—PETER F. ZIKA, BLM, P.O. Box 10226, Eugene, OR 97440.



SEGREGATION OF *HASTINGSIA SERPENTINICOLA*,  
SP. NOV. FROM *HASTINGSIA ALBA*  
(LILIACEAE: ASPHODELEAE)

RUDOLF W. BECKING

College of Natural Resources, Humboldt State University,  
Arcata, CA 95521

ABSTRACT

A new taxon, *Hastingsia serpentinicola*, is segregated from *Hastingsia alba*. The range of *Hastingsia serpentinicola* is sympatric with that of *H. alba* except for the northern Sierra Nevada where no *H. serpentinicola* has been found. *Hastingsia serpentinicola* is exclusively limited to serpentine soils. It occupies dry open hillsides and does not occur within the permanently wet, boggy habitats of *H. alba*. There is no evidence of hybridization. The segregation of *Hastingsia serpentinicola* necessitated an emended description of *H. alba*.

A systematic study of *Hastingsia* of the Klamath Mountains of Northern California (Becking et al. 1982; Becking 1986) has revealed the existence of a new species herein described.

***Hastingsia serpentinicola*** Becking, sp. nov.—TYPE: USA, Oregon, Josephine Co., Cave Junction, Eight Dollar Mt. BLM *Darlingtonia* bog, 450 m, T38S R8W sect. 28 SW $\frac{1}{4}$  of SW $\frac{1}{4}$ , long. 123°39'25"W, lat. 42°14'00"N, 28 May 1985, *R. Becking 850500* (holotype, CAS; isotypes, GH, HSC, OSC, UC, US).

Herba typice inferioris. Bulbus oblongatus, frequenter attenuatus, 23–40 mm longus, 14–21 mm diametro. Scapus unus per annum, 28.6–51.4 cm altus. Folia angusta, linearia, 19.6–34.5 cm longitudinis maximae et 4–6 mm latitudinis maximae. Racemi terminales cum 24–35 floribus, 3.8–12 cm longi, erecti, solitarii, rarifer ramicantes. Tepala angustiae, albae, pallidae viridae vel flavae, 5–6 mm longae, 1–2 mm latae, pauce oblanceolatae, acuminatae, fortiter reflectae cum staminibus extrudentibus. Capsula oblonga, 5–8 mm longa, 4–6 mm lata.

Perennial small herbs. Bulb oblong, 23–40 mm long and 14–21 mm wide. Scape slender, solitary, 286–514 mm tall, its basal peduncle thickness 1–3 mm. Leaves grasslike, distinctly keeled, grayish green, glabrous, with 19.6–34.5 cm maximum leaf length, and 4–6 mm maximum leaf width. Terminal racemes slender, relatively open, with 24–35 flowers. Racemes 3.8–12 cm long, usually solitary, occasionally with 1–3 much shorter lateral ascending racemes. Tepal segments all nearly alike, light greenish to light yellowish-white, linear 5–6 mm long, 1–2 mm wide with a greenish-yellow or light purple central vein. Tepals sharply reflexed fully about  $\frac{2}{3}$  or more of their length. Stamens exerted, straight, 5–6 mm long; anthers



light purple becoming brownish-yellow when shedding pollen. Capsule oblong, 5–8 mm long and 4–6 mm wide. Seed wrinkled, black, 4–5 mm in length (Fig. 1).

*Paratypes.* USA, OR, Curry Co., Collier Creek, 28 Jun 1929, *Leach s.n.*, 2411, 2412 (ORE); Josephine Co., W of O'Brien, 5 Jul 1939, *Hitchcock and Martin 5166* (CAS, NY, UC); CA, Del Norte Co., Gasquet, Old Gasquet Toll Rd, 5 Jun 1965, *Roderick s.n.* (Jeps) [ $n=26$ ,  $n=27$ , Cave (1970) chromosome voucher 6775]; Humboldt Co., Willow Creek, Horse Mt., 23 Jul 1979, *Overton and Butler 9473* (HSC); Lake Co., Hulville, 2 Aug 1902, *Heller 6013* (DS, GH, NY, POM); Mendocino Co., Laytonville, Red Mt., Jun 1867, *Bolander s.n.* (DS); Trinity Co., Peanut, Philpot Creek, 13 Jun 1951, *Bacigalupi and Constance 3392* (UC).

*Distribution and ecology.* *Hastingsia serpentinicola* is limited to the Klamath Mountains and North Coast Ranges from low to high elevations. It is almost exclusively limited to ultramafic or serpentine rock outcroppings. It occupies open sites in the Klamath Mountains that are moist in the spring but dry out rapidly in the early summer (Fig. 3). It occurs along the edges of wet bogs or in the drier islands within the bog environment. At high elevations (above 1800 m) on exposed serpentine ridges it favors mesic habitats.

*Hastingsia alba* (Durand) S. Watson, Proc. Amer. Acad. Arts 14: 242, 1879, emend. Becking. — *Schoenolirion album* Durand, J. Acad. Nat. Sci. Philadelphia (Ser. #2) 3:103, 1855. The *Hastingsia alba* holotype material is very fragmentary, consisting only of a few raceme stalks and flowers collected from several individual plants. This “holotype” material was later divided into 3 portions and deposited by Durand himself into three different herbaria (P-DU, PH!, NY!). The Paris, France (P-DU) material was judged to be too fragile for overseas shipment and has not been available (S. Barrier, letter 17 Jun 1987). Because there is no longer a single intact holotype, there are consequently no isotypes (G. Zijlstra ICBN (U), letter 1 Jun 1987; B. C. Stone (PH), letter 12 Aug 1987). The PH material is designated here-with as lectotype because Durand described his “holotype” material during his tenure at the PH herbarium. The P-DU and NY material become isolectotypes. The PH material still contained a single fully intact flower, representing “a portion of the type material collected by H. Pratten in the vicinity of Deer Creek, California, 1851”, according to the typed label information.

Perennial herb, often robust. Bulb 26–56 mm long, 17–31 mm wide. Scape robust, 40.4–89 cm tall, basal thickness of the peduncle 3–5 mm. Leaves glaucous green, changing with age to light green,





FIG. 1. *Hastingsia serpentinicola*. a, Fruiting plant; b, flowering plant; c, stamens; d, frontal view of flower; e, pistil; f, part of flowering raceme; g, longitudinal section of flower; h, fruiting raceme; i, part of fruiting raceme; j, cross-section of capsule; k, longitudinal section of capsule; l, seeds; m, longitudinal section of seed. All bar scales = 10 mm.



more fleshy, keeled, 27.8–53 cm long and 7–14 mm wide. Racemes compact, 8–20.3 cm long, densely flowered with 62–75+ flowers, often 2–3 branched, erect and terminal. Perianth segment pure white, sometimes slightly yellowish-white, obtuse, rotate at about half of the tepal length, giving the opened perianth a distinct star-shaped appearance. Basal portion of the perianth bell-shaped when closed. Outer 3 tepals linear, 6–8 mm long and 1 mm wide, ending in a blunt, slightly swollen white tip. Inner 3 tepals ovate, 6–8 mm long and 2 mm wide, often with a crisped margin. Stamens only slightly protruding beyond the perianth, anthers often purplish. Filaments 6–7 mm long. Outer 3 stamens opposite the ovate tepals, usually elongate, and open first; the 3 inner stamens elongate on following days and become almost of equal length to the outer stamens when their anthers dehisce. If the flower has just opened, it appears that for the first days the 3 outer stamens have long filaments whereas the inner stamens have short filaments. Capsule oblong, broadly 3-lobed, 6–9 mm long, and 5–8 mm wide. Seed wrinkled, black, 4–6 mm long (Fig. 2).

*Representative specimens.* USA, OR, Curry Co., Vulcan Lake, 23 Jul 1978, *Dawn* 47 (OSC); Josephine Co., Cave Junction, Illinois River bridge USFS Road 3843, 17 Jun 1982, *Becking* 820600 (HSC); CA, Butte Co., Jonesville, 22 Jul 1914, *Hall* 9769 (NY); Del Norte Co., Steven Mt., 3 Aug 1980, *Baker* 3577 (HSC); Humboldt Co., Hoopa, Mill Creek Lakes, 1 Aug 1979, *Clifton and Griswold* 11944 (HSC); Nevada Co., Willow Springs, 26 Jun 1961, *Cruden* 1035 (JEPS) [ $n=26$ , Cave 1966, 1970]; Plumas Co., N Fork Feather River, Mosquito Creek, 1 Jul 1965, *See s.n.* (JEPS) [ $n=26$ , Cave 1970]; Shasta Co., Delta, Sacramento River, 18 Jun 1923, *Bethel s.n.* (CAS); Siskiyou Co., Callahan, French Creek Rd, 12–16 Jun 1948, *Ferris and Lorraine* 11730 (ORE, NY, RSA, DS); Tehama Co., Deer Creek Canyon, 17 Jul 1911, *Eggleston* 7265 (NY); Trinity Co., Denny, New River-Trinity River confluence, 17 May 1975, *Sullivan* 65 (HSC).

*Distribution and ecology.* *Hastingsia alba* is not predominantly a species of the Klamath Mountains Geological Province (Ramp and Peterson 1979; Borine 1983; Ferlatte 1974). It has been collected in numerous other locations in the North Coast Ranges and the northern Sierra Nevada. In both situations it occurs on serpentine, on granite, and diorite. It occupies most commonly open rocky seepage areas with a year-round water supply, or bogs or wet meadows, especially at high elevations. Its elevation ranges from 500–2300 m. At high elevations, *H. alba* is often stunted and has smaller bulbs, shorter scapes, and shorter and narrower leaves. The other floral and capsule distinctions, however, are retained (Fig. 3).





FIG. 2. *Hastingsia alba*. a, Fruiting plant; b, flowering plant; c, top of flowering raceme; d, longitudinal view of flower; e, longitudinal section of flower; f, cross-section of leaf; g, flowering plant, robust form; h, top of flowering raceme; i, part of fruiting raceme; j, longitudinal section of capsule; k, cross-section of capsule; l, seeds and longitudinal section of seed. All bar scales = 10 mm.



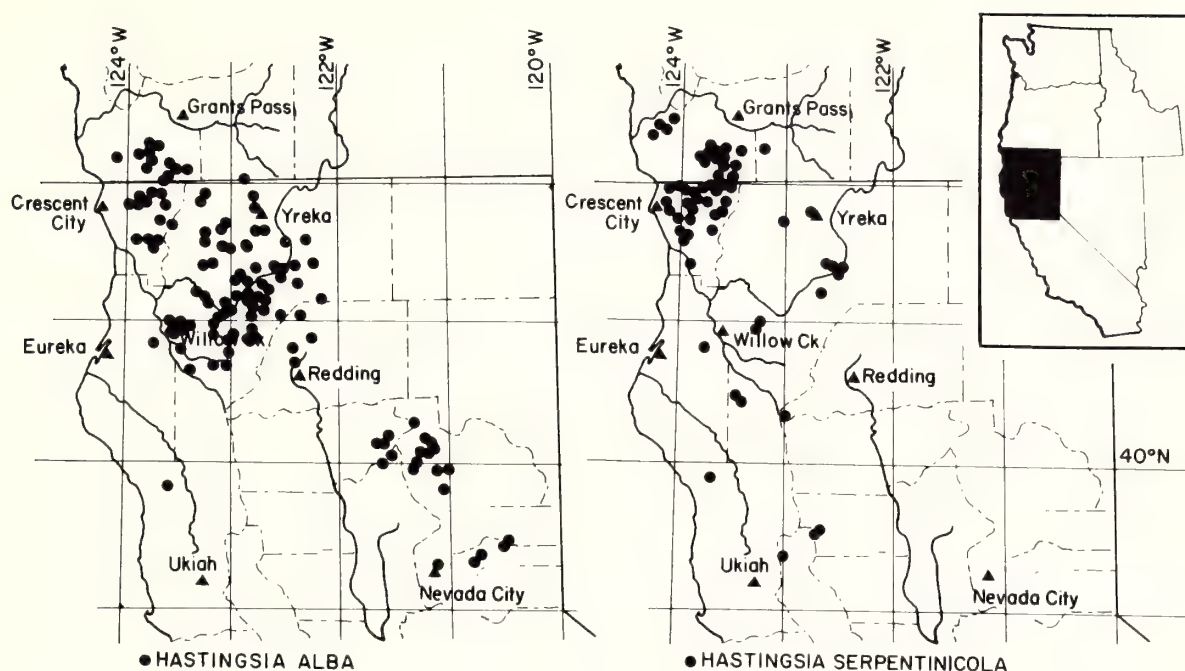


FIG. 3. Distribution of *Hastingsia serpentinicola* and *H. alba*.

#### COMPARISON OF *HASTINGSIA SERPENTINICOLA* AND *H. ALBA*

*Statistical analyses.* Comprehensive t-test analyses for unequal variances were applied to the 442 measured specimens selecting the 47 characters for comparison at the individual character level. Twelve most significant characters out of the total 33 significant characters at the 0.01 probability level are identified in Table 1.

Two discriminant analyses (Nie et al. 1975; Dixon et al. 1983) were used independently to classify the 196 herbarium specimens of *Hastingsia serpentinicola* and the 246 specimens of *H. alba*. Thirty-nine quantitative and eight qualitative characters were selected in these tests by the computer programs. All the specimens missing one or more characters of this character set were disqualified from the discriminant analysis. Because of this potential for many unwarranted exclusions, the number of characters had to be selectively limited to increase the number of qualifying cases. Rarely one finds fully developed flowers and mature capsules together on the same individual herbarium specimen or field specimen. Five character groupings were selected using various combinations of bulb, scape, foliage, flower and capsule characters (Table 2). The segregations into the two species were supported by both computer programs in all the character groupings tested (canonical  $r^2 = 0.824\text{--}0.984$ , 86–100% correct classification).

Foliage and bulb characters of *Hastingsia alba* performed the poorest among herbarium specimens when either discriminant program was applied. Collectors tend to choose small individuals to



TABLE 1. DISTINCTIONS BETWEEN *HASTINGSIA SERPENTINICOLA* AND *H. ALBA*. All characters listed had significant differences at the 0.01 probability level by t-test analysis. Leaf width was measured selectively on 2–3 undamaged leaves at about the middle of the leaf length to establish the maximum and minimum dimension. "Raceme open" length was measured from the top of the terminal raceme to the lowest lateral raceme branch or the lowest flower in the terminal raceme. "Raceme dense" length was measured from the top of the terminal raceme to where the interspatial distances between the flower pedicels exceeded the length of the perianth. Density of flowers counted the numbers per 5 cm length of the terminal raceme and expressed this count per 10 cm raceme length. The densest (top most portion) and the least sparse (basal portion) raceme portions were selected for counting the maximum/minimum range of flower density respectively. The number of cases involved is indicated in parentheses.

|                     | <i>H. serpentinicola</i> | <i>H. alba</i>     |
|---------------------|--------------------------|--------------------|
| Bulb length         | 23.2–40.2 mm (150)       | 26.3–55.9 mm (164) |
| Bulb diameter       | 13.5–21.1 mm (150)       | 17.3–31.3 mm (164) |
| Scape length        | 28.6–51.4 cm (196)       | 40.4–89.0 cm (237) |
| Leaf length max.    | 19.6–34.5 cm (194)       | 27.8–52.9 mm (241) |
| Leaf width max.     | 3.5–5.7 mm (194)         | 7.4–13.6 mm (241)  |
| Tepal length max.   | 4.9–6.3 mm (189)         | 5.5–7.5 mm (213)   |
| Tepal width max.    | 0.9–1.9 mm (189)         | 1.7–2.3 mm (213)   |
| Raceme open length  | 4.5–26.7 cm (192)        | 13.7–39.8 cm (243) |
| Raceme dense length | 3.8–12.0 cm (192)        | 8.0–20.3 mm (243)  |
| Flower density max. | 28.3–48.5 mm (160)       | 38.6–63.6 mm (207) |
| Flower density min. | 21.7–41.9 mm (131)       | 32.4–56.2 mm (205) |
| Capsule length max. | 4.7–7.5 mm (061)         | 5.7–9.3 mm (098)   |
| Capsule width max.  | 3.6–6.0 mm (061)         | 4.5–7.7 mm (098)   |

press and often remove the dead and shriveled black basal leaves. Extraction of bulbs at depths of 25–45 cm often leaves the tunica in the soil. Only older specimens develop the typical tunica, whereas younger and smaller specimens do not. The bulbs are often cut or squashed making it most difficult to obtain representative measurements. Capsules are often immature. Only fully matured capsules with black seeds are dimensionally representative. In segregations based upon herbarium specimens, *H. serpentinicola* was classified more consistently than *H. alba* (85–100% correct classification). In mature and fresh specimens, however, such misclassifications were rarely encountered.

*Distinction between species.* In past treatments (Jepson 1921, 1936; Abrams 1923; Mason 1957; Munz 1959; Peck 1961; Ferlatte 1974) *Hastingsia serpentinicola* has not been segregated from *H. alba*. Stature and size differences were attributed to harsh environmental conditions. However, Roderick, in 1965, annotated his collections of *H. serpentinicola* (JEPS) as distinct from *H. alba*. He further noted that plants now attributed to *H. serpentinicola* occur "almost always on serpentine on well-drained soil never in a bog".

Both *Hastingsia* species were cultivated for many years in the Botanical Garden at UC Berkeley, CA. Growing both in the same



TABLE 2. DISCRIMINANT ANALYSES USING 246 SPECIMENS OF *HASTINGSIA ALBA* AND 196 SPECIMENS OF *H. SERPENTINICOLA*. The first two lines per category represent the SPSS90 program results, the third line the BMDP83 results, using identical data sets. 1) # char = the number of characters selected by the program for classification into the grouping. 2) (#\*) = the number of most significant characters selected within the character grouping for the final classification function. 3) # cases = the number of cases selected with complete character sets within the grouping. 4) canon. r% = canonical correlation coefficient of the final classification function. 5) *H. a.* and *H. s.* = *Hastingsia alba* and *H. serpentinicola*, respectively. 6) % class (#) = percent of correct classification (number of cases involved). 7) J = Jackknife classification using Mahalanobis D<sup>2</sup> (BMDP83). 8) W = Wilk's Lambda (SPSS90) classification.

| Character groupings                   | <sup>1</sup> # char,<br><sup>2</sup> (#*) | <sup>3</sup> # cases | <sup>4</sup> canon. r% |                 | Percent correctly classified                          |                             |                  |
|---------------------------------------|---|----------------------|------------------------|-----------------|---|-----------------------------|------------------|
|                                       |   |                      |                        |                 | <sup>5</sup> <i>H. a.</i><br><sup>6</sup> % class (#) | <i>H. s.</i><br>% class (#) | Total<br>% class |
| Bulb, scape, foliage                  | 10  | 298                  | 0.824                  |                 | 86.3 (153)  | 100.0 (145)                 | 93.0             |
|                                       | (2*)                                      |                      |                        | <sup>7</sup> J: | 86.3 (153)  | 100.0 (145)                 | 93.0             |
|                                       | 10  | 298                  | 0.824                  | <sup>8</sup> W: | 87.9 (224)  | 100.0 (194)                 | 93.5             |
| Foliage, scape                        | (4*)                                      |                      |                        |                 |   |                             |                  |
|                                       | 8   | 411                  | 0.824                  |                 | 87.8 (222)  | 100.0 (189)                 | 93.2             |
|                                       | (4*)                                      |                      |                        | J:              | 87.4 (222)  | 100.0 (189)                 | 93.2             |
| Foliage, scape, flower                | 8   | 411                  | 0.824                  | W:              | 87.9 (224)  | 100.0 (194)                 | 93.5             |
|                                       | (4*)                                      |                      |                        |                 |   |                             |                  |
|                                       | 26  | 232                  | 0.984                  |                 | 99.3 (135)  | 99.0 (097)                  | 99.1             |
| Foliage, scape, capsule               | (3*)                                      |                      |                        | J:              | 99.3 (135)  | 99.0 (097)                  | 99.1             |
|                                       | 26  | 232                  | 0.985                  | W:              | 97.9 (188)  | 84.9 (179)                  | 91.6             |
|                                       | (7*)                                      |                      |                        |                 |   |                             |                  |
| Bulb, scape, foliage, flower, capsule | 14  | 92                   | 0.873                  |                 | 95.0 (060)  | 100.0 (032)                 | 96.7             |
|                                       | (3*)                                      |                      |                        | J:              | 95.0 (060)  | 100.0 (032)                 | 96.7             |
|                                       | 14  | 92                   | 0.885                  | W:              | 98.3 (064)  | 100.0 (032)                 | 98.9             |
|                                       | (5*)                                      |                      |                        |                 |   |                             |                  |
|                                       | 47  | 30                   | 0.972                  |                 | 100.0 (018)   | 100.0 (012)                 | 100.0            |
|                                       | (6*)                                      |                      |                        | J:              | 100.0 (018)   | 100.0 (012)                 | 100.0            |
|                                       | 47  | 37                   | 0.999                  | W:              | 95.5 (022)  | 86.7 (015)                  | 91.9             |
|                                       | (18*)                                     |                      |                        |                 |   |                             |                  |

rich garden soil, the cultivated specimens produced flowers and viable seeds (W. Roderick, letter 24 Dec 1985) and retained their distinctive characters, suggesting no environmental influences upon these morphological characters. *Hastingsia serpentinicola* did not flourish well, however, in Berkeley, with its mild winters and hot dry summers. Herbarium specimens of these cultivated *Hastingsia* plants served as voucher specimens for pollen collection and chromosome counting (Cave 1966, 1970).

ACKNOWLEDGMENTS

Curators of the various herbaria (CAS, DAV, DS, GH, HSC, JEPS, NY, ORE, OSC, PH, PUA, ROPA, RSA, SOC, UC) are acknowledged for their hospitality during visits and loan of specimens. Acknowledged are the constructive comments of Dr. F. Raymond Fosberg (NAT), Dr. M. G. McLeod, Dr. Robert Peet (NC), Dr. Wm. A. Weber (CO), 9 anonymous reviewers and 2 editors.



## LITERATURE CITED

- ABRAMS, L. 1923. An illustrated flora of the Pacific states, vol. 1. Stanford Univ. Press, Stanford, CA.
- BECKING, R. W. 1986. *Hastingsia atropurpurea* (Liliaceae, Asphodeleae), a new species from southwestern Oregon. *Madroño* 33:175–181.
- BECKING, R. W., J. A. LENIHAN, and E. MULDAVIN. 1982. Final report. *Schoenolirion bracteosum*. Ecological investigations. Contract #43-9A4-0-1645. Six Rivers Nat. Forest, Eureka, CA.
- BORINE, R. 1983. Soil survey of Josephine County, Oregon, USDA Soil Conservation Service, Grants Pass, OR.
- CAVE, M. S. 1966. In Documented chromosome numbers of plants. *Madroño* 18: 245–246.
- . 1970. Chromosomes of the California Liliaceae. *Univ. Calif. Publ. Bot.* 57: 8, 10.
- DIXON, W. J., (chief ed.) et al. 1983. BMDP statistical software 1983 printing with additions. 18.4 Stepwise Discriminant Analysis P7M:519–537. Univ. Calif. Press, Berkeley, CA.
- DURAND, E. 1855. *Plantae Prattenianae Californicae*. *J. Acad. Nat. Sci. Philadelphia* (Ser. 2)3:103.
- FERLATTE, W. J. 1974. A flora of the Trinity Alps of northern California. Univ. Calif. Press, Berkeley.
- JEPSON, W. L. 1921. A flora of California, vol 1, part 6. Assoc. Students Store, Univ. California Berkeley.
- . 1923–1925, 1936. A manual of the flowering plants of California. Assoc. Students Store, Univ. California Berkeley.
- MASON, H. L. 1957. A flora of the marshes of California. Univ. Calif. Press, Berkeley.
- MUNZ, P. A. 1959. A California flora. Univ. California Press, Berkeley.
- NIE, N. H., C. H. HULL, J. G. JENKINS, K. STEINBRENNER, AND D. L. BENT. 1975. SPSS: statistical package for the social sciences, pp. 434–467. McGraw-Hill, Inc, New York.
- PECK, M. E. 1961. A manual of the higher plants of Oregon. Metropolitan Printing Co., Portland, OR.
- RAMP, L. AND N. V. PETERSON. 1979. Geology and mineral resources of Josephine County, Oregon. Dept. Geology & Mineral Resources, State of Oregon. Bull. 100.
- WATSON, S. 1879. Revision of the North American Liliaceae. *Proc. Amer. Acad. Arts* 14:213–288.
- . 1885. *Hastingsia bracteosa* S. Wats. *Proc. Amer. Acad. Arts* 20:377.

(Resubmitted 12 Sep 1988; revision accepted 9 Mar 1989.)



## NOTE

*ISOPYRUM STIPITATUM* A. GRAY (RANUNCULACEAE) IN THE WILLAMETTE VALLEY, OREGON.—This inconspicuous perennial herb has been collected from only three localities in the Willamette Valley, where it is at the northern limit of its known distribution. The species is also known from the Klamath-Siskiyou region of Oregon and California, southward into the Cascades and northern Coast Ranges of California, and is disjunct at its southern limit in the East Bay region of Alameda and Santa Clara Counties (Calder and Taylor, Madroño 17:69–76, 1963). In *Rare, Threatened and Endangered Plants and Animals of Oregon* (Oregon Natural Heritage Data Base, 1989) *I. stipitatum* is currently included on the review list, which comprises species for which more information is needed before their status can be determined.

The first Willamette Valley collections were from Yamhill County, where *I. stipitatum* was collected on 5 occasions between 1957 and 1959 along Willamina Creek, north of Willamina [7 Mar 1957, Mendenhall s.n. (OSC)]. The species is still extant in this locality, though the number and extent of colonies has declined in recent years (E. Mendenhall, pers. comm.). A 1958 collection from Polk County [31 Jan 1958, Lofgren s.n. (OSC)] was taken from Buell County Park, along Mill Creek about 12 km SE of the Yamhill County locality. The most recently discovered population, along the Marys River south of Corvallis, Benton County [30 Mar 1980, Chambers 4602 (OSC)] appears to have been extirpated. The circumstances surrounding the Polk County occurrence, which is still extant [7 Apr 1988, Alverson 1306 (OSC)], seem sufficiently unusual to warrant a description.

In the Willamette Valley *I. stipitatum* appears to occur primarily in rich deciduous woods that occupy alluvial stream bottoms. Herbarium labels and field observations show that *Acer macrophyllum* and *Fraxinus latifolia* dominate the tree canopy of such sites, with a diverse herb layer typified by *Delphinium trolliifolium*, *Hydrophyllum tenuipes*, *Viola glabella*, *Thalictrum occidentale*, and *Trillium albidum*. The diminutive *I. stipitatum* occupies open microsites amongst the generally thick herbaceous cover. At Buell Park, *I. stipitatum* could not be found in such natural woodlands, but instead occurred in sizable patches in the rough lawn of an adjacent picnic area and playground, over an area of about 0.5 ha. *Isopyrum* was most abundant and vigorous under the canopies of scattered trees of *Fraxinus* and *Acer*, where competing grasses were relatively sparse. The remnant trees of *Fraxinus* and *Acer* suggest that this area was also alluvial deciduous woodland at one time. It is plausible that *I. stipitatum* was present at the site before the park was established, and has persisted, or perhaps even increased, with the removal of competing native shrubs and herbs. Interestingly, the habit of persisting in lawns and pastures has been reported for *Isopyrum biternatum*, a species of eastern North America (Korling, *Eastern Deciduous Forest*, 1973).

The small stature of the plants and the early blooming season (mostly February and March) are perhaps partially responsible for the paucity of known occurrences of *I. stipitatum* in northwestern Oregon. Additional populations may possibly occur undetected elsewhere in the Willamette Valley, particularly in alluvial stream bottom habitats. However, care should be taken to ensure that the few known populations are not needlessly destroyed.

I thank Elizabeth Mendenhall for providing access to *I. stipitatum* colonies, as well as information on their original discovery, and the Mazamas Research Committee for providing funds supporting field work—EDWARD R. ALVERSON, Department of Botany and Plant Pathology, Oregon State University, Corvallis, OR 97331. (Received 22 Nov 1988; revision accepted 30 May 1989.)



## COMMENTARY

### POINTS OF VIEW: RESPONSE TO REVEAL

The report of David Douglas's death (Reveal, *Madroño* 36:137–140, 1989), to paraphrase Mark Twain, has been exaggerated. Nothing that editors can do, fortunately, will change the honor owed to and bestowed upon that intrepid explorer.

Reveal argues that botanical honor accrues from authorship of names. I believe that this view is both faulty and dangerous.

It is faulty because many standardly used names were not proposed by the foremost expert in the group. As one common kind of example (portrayed here in an extreme form), consider that the greatest contribution to botanical knowledge in a group was made by a botanist who, after years of detailed study, reduced many unjustifiable specific epithets to varietal rank. Soon after, another botanist, compiling a manual, decided to use those names and circumscriptions at subspecific rank. Accordingly, he recombined all the names of the expert botanist, leaving the expert's name unattached as author to any epithets in the group to which he devoted his life. This unfairness is required by the rules of nomenclature, which have no concern with *recognition* of individuals.

Furthermore, Reveal's assumption of honor-to-the-author is dangerous because it leads individuals to wish their names attached to a large number of taxa as a measure of their great contribution to systematic botany. Over the long run, no urge could be more counterproductive to the accepted goal of stability of scientific names.

Citation of persons in addition to the publishing author (as allowed through proper use of "in" and "ex") serves a historical function but not a nomenclatural one. Given serious constraints on space, the editors of *The Jepson Manual* chose to leave explication of botanical history to authors and works able to focus adequately on this important and fascinating subject. We chose instead to concentrate on allowing the easiest possible identification of California plants, with the most accurate possible morphological and range descriptions.

In *The Jepson Manual*, David Douglas will be listed as author only rarely—for those names that he actually published. But his name will be repeated many times, commemorated in common names and specific epithets appropriate to his pioneering work.—JAMES C. HICKMAN, Jepson Herbarium, University of California, Berkeley, CA 94720.

## ANNOUNCEMENT

### TEMPORARY NEW ADDRESS FOR EDITOR OF MADROÑO

From 1 September 1989 to 18 December 1989 Dr. David J. Keil, Editor of *MADROÑO*, will be on sabbatical leave. Manuscripts, proofs, and other correspondence should be sent to:

DR. DAVID J. KEIL  
Department of Botany  
Arizona State University  
Tempe, Arizona 85287



## REVIEWS

*Soil-Plant Relations: An Ecological Approach.* By D. W. JEFFREY. Croom Helm, London and Sydney, and Timber Press, Portland, OR. 1987. 295 pp., \$26.95 (paper); \$33.95 (hardbound).

The below-ground environment for plants is too often overlooked by botanists. Despite the plethora of research papers, symposia and books on the soil-plant interface, it largely remains the domain of the specialist. It is refreshing, therefore, to encounter a generalist's guidebook to this important earthy subject. Jeffrey's book looks at the soil-plant system, not from a greenhouse or agricultural view, but from an ecological one.

The book's three parts follow a logical and didactic progression: From the essentials of the soil-plant context, to soils and mineral nutrition, and finishing with a selection of case histories. The first of the three sections (Part I, "A plant-centered biological complex") gives the reader the fundamentals of plant and soil physiology: ion uptake, inorganic mineral nutrition of plants, water uptake. Further along in this section are chapters on mycorrhizal and other symbioses, biomass recycling, and a précis on fire in the soils-vegetation mix.

Part II focuses on the soil component of the soil-plant syndrome. Good accounts of soils formation, the microenvironment of soils (matrix temperature and nutrient supply) now follow. Ch. 11 deals with the critical issues of nutrient availability and toxic ions, and Ch. 12 explores techniques used in testing for soil variables.

Part III is a refreshing departure. Rather than an attempt at rounding out an encyclopedic coverage, of yet other topics, Jeffrey adopts the case-history approach. Each one of the seven chapters deals with a specific and significant issue in soils-vegetation studies: 1) Autecology of contrasting species, 2) Restoration of derelict land, 3) Heathlands and other nutrient-poor ecosystems, 4) Arctic tundra, 5) Salt marshes, 6) Calcareous, and 7) serpentine plant-soil relations. It is in this section that Jeffrey builds an ecological edifice from the substance of the earlier chapters. The selection of case-histories is judicious, and tells a fascinating story.

All in all the book ably fills a significant niche in telling of the all-important relations between soils and plants. The North American co-publisher, Timber Press, is to be commended in supporting this worthy contribution. — A. R. KRUCKEBERG, University of Washington, Seattle, WA 98195.

---

*North American Terrestrial Vegetation.* Edited by MICHAEL G. BARBOUR and W. DWIGHT BILLINGS. Cambridge University Press, New York. 1988. 434 pp., \$49.50 (hardbound). ISBN 0-521-26198-8.

At Last! Barbour and Billings have put together the state-of-the-art compilation of the vegetation of North America. Though they discuss in the preface how they started in 1982 on a three year project to produce this book, the need for such a volume has been talked about for the past twenty years. They are to be commended for the successful completion of a very difficult task.

The success of this publication is in large part due to the team of writers that Barbour and Billings were able to gather. The thirteen chapters are authored by a veritable "who's-who" of vegetation scientists on this continent: Bliss—Arctic, Elliott-Fisk—boreal forest, Peet—Rocky Mountains, Franklin—Pacific Northwest, Bar-



bour—California forests and woodlands, Keeley and Keeley—Chaparral, West—intermountain shrublands and woodlands, MacMahon—warm deserts, Sims—grasslands, Grellier—deciduous forests, Christensen—coastal plain, Hartshorn—tropical and subtropical forests, and Billings—alpine.

Each of the chapters deals in general with the topics of vegetation structure and composition, response to disturbance, variations due to environmental gradients, autecology of selected species, vegetational history, and suggestions for future research. These chapters are individualized, however; each one with a slightly different emphasis based on the authors' experience and bias and upon the main thrust of the research accomplished in the specific vegetation type. Examples are the emphasis on species in the chapter on chaparral, the emphasis on forest types in the chapter on Pacific Northwest, and the emphasis on community-environment relations in the chapter on arctic vegetation.

This book could not possibly have reviewed all the work in vegetation science in North America, no one book could do that. For instance, Peet, in his excellent review of the forests of the rocky mountain region, mentions *Populus tremuloides* only in the context of its being a "montane seral forest" type. Mueggler, in a study of aspen forest types in the rockies (USDA Forest Service, Gen. Tech. Report INT-250), however, lists 14 major, 12 minor, and 33 incidental aspen community types. No one should approach this book with the idea that it will answer all questions on any given vegetation, it won't. We will still have need of more in-depth, regional works. This is an overview look at the plant cover of the continent and as such it is excellent.

Even when one comes to this book in the right frame of mind, there are some disappointments. Most of the chapters treat the subject as if we were still in the days of Daniel Boone or even George Washington. I found myself on a number of occasions wanting to see the authors discuss the intrusion of man into the system with the resulting isolation of "natural" or "pristine" areas. As we all know from our treks about the country-side, it is getting harder and harder to find good examples of many plant communities in natural condition. This issue is so little dealt with that it hinders the book's usefulness to those that are traveling outside their normal sphere of experience.

The second disappointment to me is the lack of reference to major regional mapping, such as Brown and Lowe's *Biotic communities of the Southwest* (1980, USDA Forest Service Gen. Tech. Rep. RM-78) and the many classification efforts that are ongoing, especially here in the west. More recognition should have been given to these kinds of work and it would have made the book more useful to have them referenced.

In their preface the authors state that their intended audience is knowledgeable laypeople, advanced undergraduates, graduate students, and professional ecologists in both basic and applied fields. It's stretching things a bit to think that a layperson will pay the price for a fairly large book without glossy pictures and maps to tell them where to go and see, but this book is a must for every field biologist of whatever ilk. In 1960 we all ran around with Oosting's *Plant Ecology*, in 1990 we'll have Barbour and Billings' *North American Terrestrial Vegetation*. — WILLIAM L. HALVORSON, Channel Islands National Park, Ventura, CA 93001.



## SUBSCRIPTIONS—MEMBERSHIP

Membership in the California Botanical Society is open to individuals (\$22 per year; students \$12 per year for a maximum of seven years). Members of the Society receive MADROÑO free. Family memberships (\$25) include one five-page publishing allotment and one journal. Emeritus rates are available from the Corresponding Secretary. Institutional subscriptions to MADROÑO are available (\$30). Membership is based on a calendar year only. Applications for membership (including dues), orders for subscriptions, and renewal payments should be sent to the Treasurer. Requests and rates for back issues, changes of address, and undelivered copies of MADROÑO should be sent to the Corresponding Secretary.

## INFORMATION FOR CONTRIBUTORS

Manuscripts submitted for publication in MADROÑO should be sent to the editor. All authors must be members, and membership is prerequisite for review.

Manuscripts and review copies of illustrations must be submitted in triplicate for all articles *and* short items intended for NOTES AND NEWS. Follow the format used in recent issues for the type of item submitted and allow ample margins all around. All manuscripts **MUST BE DOUBLE SPACED THROUGHOUT**. For articles this includes title (all caps, centered), author names (all caps, centered), addresses (caps and lower case, centered), abstract, text, acknowledgments, literature cited, tables (caption on same page), and figure captions (grouped as consecutive paragraphs on one page). Order parts in the sequence listed ending with figures, and number each page. Do not use a separate cover page, "erasable" paper, or footnotes. Manuscripts prepared on dot matrix printers may not be considered. Table captions should include all information relevant to tables. All measurements should be in metric units.

Line copy illustrations should be clean and legible, proportioned (including captions) to the MADROÑO page, and designed for reduction to  $\frac{2}{3}$  original size. Scales should be included in figures, as should explanation of symbols, including graph coordinates. Symbols smaller than 1 mm after reduction are not acceptable. Maps must include latitude and longitude references. Halftone copy should be designed for reproduction at actual size. In no case should original illustrations be sent prior to the acceptance of a manuscript. When needed they should be mounted on stiff cardboard and sent flat. No illustrations larger than 22 × 28 cm will be accepted.

Presentation of nomenclatural matter (accepted names, synonyms, typification) should follow the format used for *Rhus integrifolia* in MADROÑO 22:288. 1974. Institutional abbreviations in specimen citations should follow Holmgren, Keuken, and Schofield, Index Herbariorum, 7th edition. Abbreviations of serial titles should be those in Botanico-Periodicum-Huntianum (Lawrence et al., 1968, Hunt Botanical Library, Pittsburgh). If the correct abbreviation cannot be determined, the full serial title should be used. Titles of books should be given in full, together with the place and date of publication, publisher, and edition, if other than the first.

All members of the California Botanical Society are allotted five free pages per volume in MADROÑO. Joint authors may split the full page number. Beyond that number of pages a required editorial fee of \$65.00 per page will be assessed. The purpose of this fee is not to pay directly for the costs of publishing any particular paper, but rather to allow the Society to continue publishing MADROÑO on a reasonable schedule, with equity among all members for access to its pages. Printer's fees for illustrations and typographically difficult material @ \$35.00 per page (if their sum exceeds 30 percent of the paper) and for author's changes after typesetting @ \$4.50 per line will be charged to authors.

At the time of submission, authors must provide information describing the extent to which data in the manuscript have been used in other papers that are published, in press, submitted, or soon to be submitted elsewhere.





CALIFORNIA BOTANICAL SOCIETY



83

MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

Contents

|  |  |
|--|--|
| TAXONOMY OF THE <i>OPUNTIA SCHOTTII</i> COMPLEX (CACTACEAE) IN TEXAS<br><i>Barbara E. Ralston and Richard A. Hilsenbeck</i>  | 221                                    |
| BIOSYSTEMATIC STUDIES OF <i>PHACELIA CAPITATA</i> (HYDROPHYLLACEAE), A SPECIES<br>ENDEMIC TO SERPENTINE SOILS IN SOUTHWESTERN OREGON<br><i>J. Stephen Shelly</i>                                   | 232                                    |
| A SYSTEMATIC AND PHYTOGEOGRAPHIC STUDY OF <i>ANTENNARIA AROMATICA</i> AND <i>A.</i><br><i>DENSIFOLIA</i> (ASTERACEAE: INULEAE) IN THE WESTERN NORTH AMERICAN CORDILLERA<br><i>Randall J. Bayer</i> | 248                                    |
| A RE-EVALUATION OF <i>BEALIA MEXICANA</i> (POACEAE: ERAGROSTIDEAE)<br><i>Paul M. Peterson</i>  | 260                                    |
| A NEW SPECIES OF <i>DAPHNOPSIS</i> (THYMELAEACEAE) FROM BAJA CALIFORNIA SUR,<br>MEXICO<br><i>Dennis E. Breedlove and José Luis León de la Luz</i>  | 266                                    |
| <i>MONARDELLA BENEOLENS</i> (LAMIACEAE), A NEW SPECIES FROM THE CREST OF THE<br>SOUTHERN SIERRA NEVADA, CALIFORNIA<br><i>James R. Shevock, Barbara Ertter, and James D. Jokerst</i>                | 271                                    |
| NOTES  |  |
| THE TAXONOMIC RELATIONSHIPS OF <i>ALLOCARYA CORALLICARPA</i> (BORAGINACEAE)<br><i>Kenton L. Chambers</i>   | 280                                    |
| COMMENTS AND NOTES ON <i>PORTULACA</i> IN CALIFORNIA<br><i>Walter A. Kelley</i>  | 281                                    |
| NOTEWORTHY COLLECTIONS   |  |
| CALIFORNIA   | 283                                    |
| COLORADO   | 285                                    |
| REVIEWS  | 287                                    |
| ANNOUNCEMENTS  | 231, 247, 265, 270, 279, 286, 288, 289 |
| ERRATUM  | 282                                    |
| COMMENTARY   |  |
| EDITOR'S REPORT FOR VOLUME 36  | 289                                    |
| VIEWERS OF MANUSCRIPTS   | 290                                    |
| INDEX FOR VOLUME 36  | 291                                    |
| DEDICATION   | ii                                     |
| TABLE OF CONTENTS FOR VOLUME 36  | iv                                     |
| DATES OF PUBLICATION   | 290                                    |





MADROÑO (ISSN 0024-9637) is published quarterly by the California Botanical Society, Inc., and is issued from the office of the Society, Herbarium, Life Sciences Building, University of California, Berkeley, CA 94720. Subscription rate: \$30 per calendar year. Subscription information on inside back cover. Established 1916. Second-class postage paid at Berkeley, CA, and additional mailing offices. Return requested. POSTMASTER: Send address changes to James R. Shevock, Botany Dept., California Academy of Sciences, San Francisco, CA 94118.

*Editor*—DAVID J. KEIL

Biological Sciences Department  
California Polytechnic State University  
San Luis Obispo, CA 93407

*Board of Editors*

Class of:

- 1989—FRANK VASEK, University of California, Riverside, CA  
BARBARA ERTTER, University of California, Berkeley, CA  
1990—STEVEN TIMBROOK, Ganna Walska Lotusland Foundation, Montecito, CA  
THOMAS R. VAN DEVENDER, Arizona-Sonora Desert Museum, Tucson, AZ  
1991—JAMES HENRICKSON, California State University, Los Angeles, CA  
WAYNE R. FERREN, JR., University of California, Santa Barbara, CA  
1992—BRUCE A. STEIN, The Nature Conservancy, Washington, D.C.  
WILLIAM L. HALVORSON, Channel Islands National Park, Ventura, CA  
1993—JON E. KEELEY, Occidental College, Los Angeles, CA  
RHONDA L. RIGGINS, California Polytechnic State University, San Luis Obispo, CA

---

CALIFORNIA BOTANICAL SOCIETY, INC.

OFFICERS FOR 1989-90

- President:* ROBERT W. PATTERSON, Biological Sciences Department, San Francisco State University, San Francisco, CA 94132  
*First Vice President:* NIAL F. MCCARTEN, Department of Integrative Biology, University of California, Berkeley, CA 94720  
*Second Vice President:* MARY L. BOWERMAN, 970 Second Street, Lafayette, CA 94549  
*Recording Secretary:* RODNEY G. MYATT, Department of Biological Sciences, San Jose State University, San Jose, CA 95192  
*Corresponding Secretary:* BARBARA ERTTER, University Herbarium, University of California, Berkeley, CA 94720  
*Treasurer:* MONA BOURELL, Department of Botany, California Academy of Science, San Francisco, CA 94118  
*Financial Officer:* BARRETT ANDERSON, Department of Botany, California Academy of Science, San Francisco, CA 94118

The Council of the California Botanical Society consists of the officers listed above plus the immediate *Past President*, JOHN STROTHER, University Herbarium, University of California, Berkeley, CA 94720; the *Editor* of MADROÑO; three elected *Council Members*: JAMES SHEVOCK, Department of Botany, California Academy of Science, San Francisco, CA 94118; ELIZABETH MCCLINTOCK, University Herbarium, University of California, Berkeley, CA 94720; BRUCE PAVLIK, Department of Biology, Mills College, Oakland, CA 94613; and a *Graduate Student Representative*, JAMES D. MOREFIELD, Rancho Santa Ana Botanic Garden, Claremont, CA 91711.

|   |
|---|
| THIS PUBLICATION IS PRINTED ON ACID-FREE PAPER. |
|---|



# TAXONOMY OF THE *OPUNTIA SCHOTTII* COMPLEX (CACTACEAE) IN TEXAS

BARBARA E. RALSTON<sup>1</sup> and RICHARD A. HILSENBECK  
Department of Biology, Sul Ross State University,  
Alpine, TX 79832

## ABSTRACT

Morphologic, field, and chromosomal studies of *Opuntia* series *Clavatae* including the three major taxa, *O. schottii*, *O. grahamii*, and a series of populations from Texas originally described as a putative hybrid by Anthony, suggest that *O. schottii* and *O. grahamii* are distinct and do not hybridize. The plants once considered to be hybrids are herein described as a new species, ***O. aggeria***, most closely related to *O. grahamii* and *O. moelleri*, a species from northern Coahuila, Mexico.

## RESUMEN

Estudios de campo, morfológicos y de cromosomas de *Opuntia* series *Clavatae* incluyendo las tres taxa mayor, *O. schottii*, *O. grahamii*, y una serie de poblaciones de Texas descritos originalmente como híbridos putativos por Anthony, sugieren que *O. schottii* y *O. grahamii* son distintos y que no se cruzan. Las plantas las cuales se consideran originalmente como híbridos se describen aquí como una nueva especie, ***O. aggeria***, más relacionado a *O. grahamii* y a *O. moelleri*, una especie del norte de Coahuila, México.

In *Opuntia* the series *Clavatae* (sensu Benson 1982), subgenus *Cylindropuntia*, is composed of 17 taxa in North America, the plants forming low mats or clumps. Two species, *Opuntia schottii* Engelm. and *O. grahamii* Engelm., colloquially known as club chollas, are common in southwestern Texas from the Rio Grande Plain into the Chihuahuan Desert. They have been reported to hybridize in the Big Bend Region of Texas in southern Brewster County (Anthony 1956; Benson 1982). These two species, their putative hybrid, and a single disjunct population of *O. emoryi* Engelm., constitute the *O. schottii* complex in Texas as circumscribed by Benson (1982) and Ralston (1987). Previous studies have differed in their treatments of *O. schottii* and *O. grahamii* (Britton and Rose 1919; Anthony 1956; Benson 1982; Weniger 1984). Previously, chromosome numbers for these two species were reported as  $n=11$  and  $n=22$ , respectively (Weedin and Powell 1978; Pinkava et al. 1985), indicating that speciation in the group may involve polyploidy ( $x=11$ , Benson 1982; Grant 1981). This study uses morphologic, chromosomal, and breeding system data to clarify the taxonomic and phylogenetic re-

<sup>1</sup> Present address: Department of Biology, Northern Arizona University, Flagstaff, AZ 86011.



relationships of the three major club chollas in Texas, and provides keys and descriptions for all four species (includes *O. emoryi*) of series *Clavatae* in Texas. The results of this study provide a clearer taxonomic arrangement concerning the *O. schottii* complex. The taxonomic and cytogenetic portions of the study are here presented.

### TAXONOMIC HISTORY

*Opuntia schottii* and *O. grahamii* were described from collections made during the U.S. and Mexican Boundary Survey of 1851–1853 (Engelmann 1856). The type localities for *O. schottii* and *O. grahamii* were given as “near the mouth of the San Pedro and Pecos”, and “near El Paso”, respectively. Britton and Rose (1919) maintained these species.

Since that time, however, several authors have altered the taxonomy at both the specific and generic level. Anthony (1956) described the putative hybrid, *O. schottii* × *O. grahamii* from populations in southern Brewster County, Texas. Benson (1969) reduced *O. grahamii* to a variety of *O. schottii*, apparently based on the overlapping ranges and intergrading morphology as reported by Anthony (1956). In his treatment of the complex, Weniger (1984) retained Engelmann’s taxonomy and disputed Benson’s claim of range overlap and intergradation between *O. grahamii* and *O. schottii*. Segregate genera that include these taxa have also been proposed (see synonymy), but we find no grounds, morphologic, chromosomal, or chemical, to support these alternative generic dispositions.

### HABITAT AND DISTRIBUTION

Taxa of the *O. schottii* complex grow in loosely consolidated igneous or calcareous desert alluvium, as well as on limestone outcrops. The plants grow on flats or gentle slopes and may be found both in the open or in the shade of desert shrubs, predominantly *Larrea tridentata*, *Prosopis glandulosa*, and *Acacia* spp.

In Texas, the *O. schottii* complex extends from extreme south-central New Mexico, southeastward along the Rio Grande to the Gulf of Mexico (Fig. 1). *Opuntia schottii* occupies the southern and eastern reaches of this range, from southern Brewster County to Cameron County, whereas *O. grahamii* occupies the more western and northern regions of the range (i.e., southern Brewster County to El Paso County, and the southeastern edge of New Mexico). The ranges do overlap in southern Brewster County with morphologic intergradation between the species reported there (Anthony 1956; Benson 1982). The two species also occur along the Rio Grande River in adjacent Mexico (Benson 1982). Our study, however, examined the members of the complex as they exist in Texas. The widely disjunct *O. emoryi* occurs as a single population in extreme



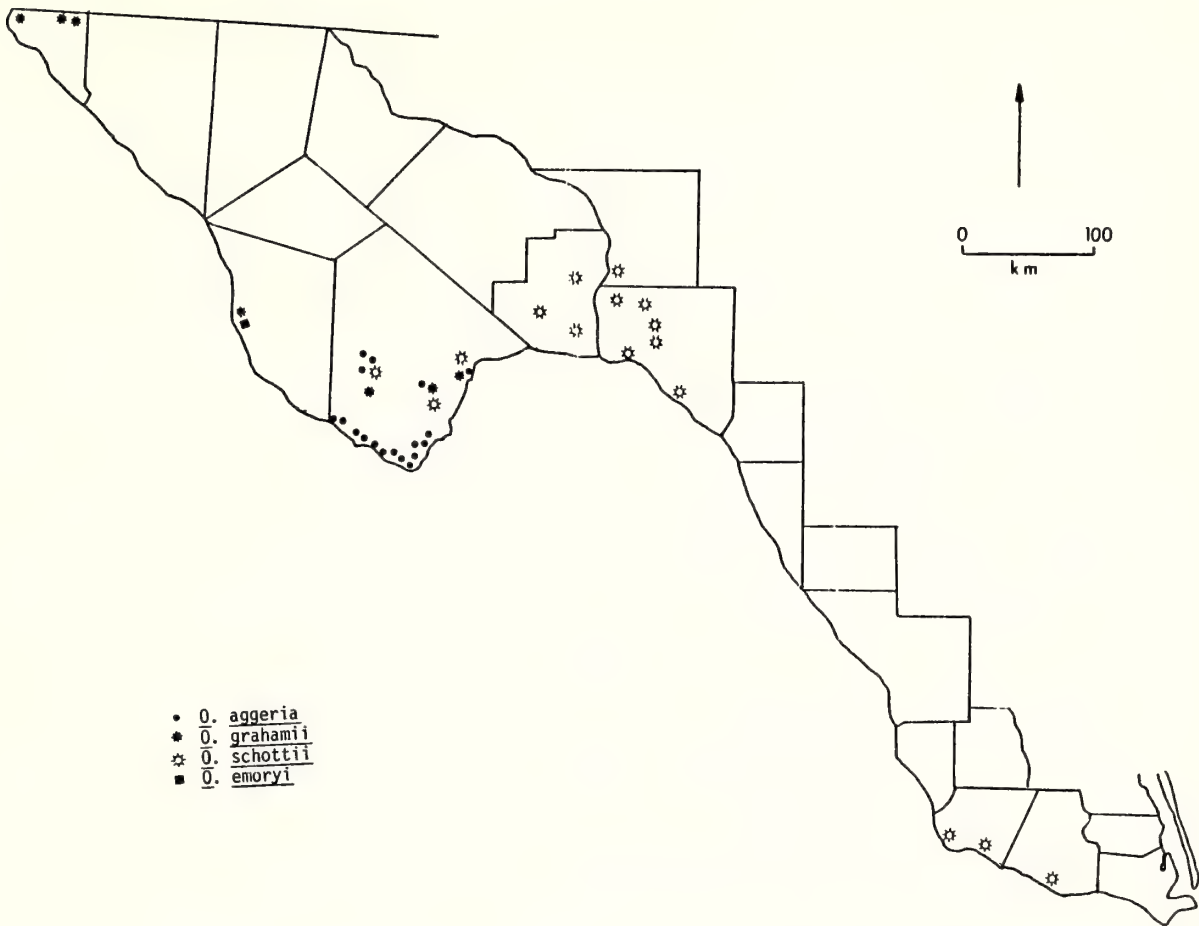


FIG. 1. Distribution of taxa in the *Opuntia schottii* complex in Texas; *Opuntia schottii* (open stars), *O. grahamii* (closed stars), *O. aggeria* (closed circles), and *O. emoryi* (closed square).

southern Presidio County and is not involved in the major taxonomic problem surrounding the complex in Texas.

#### METHODS AND MATERIALS

Population samples were collected throughout the geographic range of the complex in Texas, with particular emphasis on the area of reported intergradation in Big Bend National Park (BBNP). Vouchers are deposited in SRSC. Loans of herbarium specimens, including types, were obtained from ASU, LL, MICH, MO, POM, RSA, and TEX. Vegetative and floral characters were measured from dried and living material. Bud material for meiotic counts was collected in the field. The buds were fixed in modified Carnoy's solution (chloroform, absolute ethanol, and glacial acetic acid, 4:3:1, v:v:v).

#### RESULTS

The data in Table 1 disclose that *Opuntia schottii* is easily distinguished from *O. grahamii* by spine length and width, branching architecture, root-type, areole diameter, and relative prominence of tubercles. In Texas, *O. schottii* grows primarily east of the Pecos



TABLE 1. MORPHOLOGICAL COMPARISON OF TAXA IN THE *OPUNTIA SCHOTTII* COMPLEX IN TEXAS AND *O. MOELLERI*.

|                      | <i>O. aggeria</i>   | <i>O. emoryi</i> | <i>O. grahamii</i> | <i>O. moelleri</i>  | <i>O. schottii</i> |
|----------------------|---------------------|------------------|--------------------|---------------------|--------------------|
| Root type            | Tuberous            | Fibrous          | Tuberous           | Tuberous            | Fibrous            |
| Joint length (mm)    | 45-65               | 70-150           | 35-45              | 40-70               | 45-65              |
| Tubercle size:       |                     |                  |                    |                     |                    |
| Length (mm)          | 10-20               | 35-50            | 8-12               | 25                  | 15-20              |
| Width (mm)           | 8-10                | 10-15            | 4-6                | 15                  | 6-8                |
| Height (mm)          | 5-7                 | 10-12            | 4-6                | 10                  | 6-8                |
| Areole diameter (mm) | 3-4                 | 5-7              | 3-4                | 4                   | 5-7                |
| Spines/areole        | 7-9                 | 11-16            | 7-14               | 6-10                | 8-14               |
| Spine shape          | Flattened to terete | Flattened        | Terete             | Flattened to terete | Flattened          |
| Spine length (mm)    | 55-90               | 35-70            | 30-35              | 12-16               | 40-60              |



River and flowers much later than *O. grahamii*, which is found west of the Pecos in the United States. Populations in southern Brewster County, mostly within BBNP, designated by Anthony (1956) as putative hybrids, only occasionally exhibit intermediate characteristics or measurements between *O. schottii* and *O. grahamii* (Table 1). Measurements of *O. emoryi* and *O. moelleri* A. Berg. are also provided; the relationship of this latter species to the taxa in the complex is addressed below.

Field work in southwestern Texas indicates that the ranges of the principal taxa within the complex overlap only in southern Brewster County (Fig. 1). Two herbarium specimens identified as *O. schottii* (Weedin and Weedin 237, and Worthington 6910.5, both SRSC) suggested that this species was found in BBNP and as far west as El Paso. These specimens are now properly identified as *O. grahamii*, based on spine, joint, and root morphology.

Chromosome numbers, including previously published counts, are listed in Table 2. Chromosome numbers for *O. grahamii* and *O. schottii*, are  $n=22$  (Weedin et al. 1989; Pinkava et al. 1985). The  $n=11$  number previously reported for *O. schottii* is now correctly attributed to the putative hybrid populations from BBNP. Chromosome counts made by us for Anthony's putative hybrid populations in and around BBNP (Table 2) reveal that all populations are  $n=11$ . This number is known within the series *Clavatae* only for these populations, and for the Mexican species *O. moelleri* (Pinkava and Parfitt 1982).

The geographic and morphologic data show that although *O. grahamii* and *O. schottii* are marginally sympatric in BBNP, they do not intergrade. Additionally, the chromosomal data disclose that the putative hybrid exists at the diploid level, whereas the former two species are tetraploids. These data suggest, therefore, that the *O. schottii* complex is best treated as three species: *O. schottii* and *O. grahamii*, which show no evidence of hybridization, and Anthony's putative hybrid that is herein described as new.

TAXONOMY

KEY TO *OPUNTIA SCHOTTII* COMPLEX NORTH OF THE MEXICAN BORDER

- a Joints ovoid to obovoid; new growth emerging near apex of previous year's growth; spines mostly terete. . . . . 2. *Opuntia grahamii*
- a' Joints more or less clavate; new growth emerging from sides or bases of previous year's growth; spines mostly flattened.
  - b Spines 7–9 per areole, pink to white/gray; areoles 3–4 mm wide; roots tuberous. . . . . 1. *Opuntia aggeria*
  - b' Spines 8–16 per areole, yellow to red/brown; areoles 5–7 mm wide; roots fibrous.
    - c Plants to 8 cm high; joints 4.5–6.5 cm long; tubercles 15–20 mm long, 6–8 mm wide. . . . . 3. *Opuntia schottii*
    - c' Plants to 15 cm high; joints 7–15 cm long; tubercles 35–50 mm long, 10–15 mm wide. . . . . 4. *Opuntia emoryi*



TABLE 2. CHROMOSOME NUMBERS FOR TAXA IN THE *OPUNTIA SCHOTTII* COMPLEX AND *O. MOELLERI*. Vouchers are deposited in SRSC unless otherwise indicated. R = Ralston.

| Species            | Hap-<br>loid<br>num-<br>ber<br>(n) | Locality and Voucher   |
|--------------------|------------------------------------|--|
| <i>O. aggeria</i>  | 11                                 | TX, Brewster Co., BBNP, 19.0 km E of Castolon on River Rd, <i>R 128</i> ; BBNP, 43.4 km E of Castolon on River Rd, <i>R 135</i> ; BBNP, 33.0 km E of Castolon on River Rd, <i>R 152</i> ; BBNP, 8.4 km N of St. Elena Canyon on Maverick Rd, <i>R 114</i> ; BBNP, 5.2 km N of St. Elena Canyon on Maverick Rd, <i>R 120</i> ; BBNP, 22.0 km SE of Panther Junction, <i>R 118</i> ; BBNP, Boquillas Crossing parking area, <i>R 136</i> ; BBNP, 15.3 km W of Mariscal Mt., <i>Powell 5216</i> ; slopes of igneous hill, 0.8 km N of Lajitas, <i>Powell 5383</i> ; 15 km N of Study Butte, <i>Powell 3074a, b</i> (Weedin and Powell 1978); Lajitas arroyo bottoms, <i>Worthington 9714</i> (Pinkava et al. 1985). |
| <i>O. emoryi</i>   | 22                                 | TX, Presidio Co., 8.3 km NW of Candelaria near Capote Creek, <i>Kolle 9</i> , (Weedin and Powell 1978); 1 km N Capote Creek, <i>R 113</i> .  |
| <i>O. grahamii</i> | 22                                 | TX, Brewster Co., BBNP, Old Ore Rd near La Noria. <i>Weedin and Weedin 237</i> (Weedin and Powell 1978); El Paso Co., andesite hills, NW El Paso, <i>Worthington 6910.5</i> (Pinkava et al. 1985).   |
| <i>O. moelleri</i> | 11                                 | Mexico: Coahuila, Rte. 30, ca. 30 km S of Cuatro Cienagas Basin, at El Hundido, <i>Pinkava 13662</i> (Pinkava and Parfitt 1982).   |
| <i>O. schottii</i> | 22                                 | TX, Brewster Co., BBNP, junction of Old Ore Rd and Ernst Tinaja Rd, <i>Kolle and Weedin 53</i> (Weedin et al. 1989).   |

1. ***Opuntia aggeria*** Ralston & Hilsenbeck, nom. et stat. nov., based on *Opuntia grahamii* × *schottii* Anthony, Amer. Midl. Nat. 55: 239. 1956 (Fig. 2).—TYPE: USA, Texas, Brewster County, Big Bend National Park, on Tornillo Flats, 2800 ft, 30 Jul 1948, *M. Anthony 856* (holotype, MICH!).

Plants forming low mound to 10 cm high, 1 m wide. Roots thickened, tuberous. Branches creeping; new growth emerging from lateral areoles of previous year's growth. Joints 4–7 cm long, 2.5–3 cm in diameter. Tubercles 10–20 mm long, 8–10 mm wide, 5–7 mm high, green; areoles circular, 3–4 mm wide. Spines 7–9, mostly flattened, pink to white/gray; 3–4 spines per areole 5.5–9 cm long; 4–5 spines per areole spreading, 5–25 mm long; 2–4 radial spines deflexed; glochids numerous to 5–10 mm long. Flowers 5–7 cm long and 4–5 cm wide. Petaloids in 3–4 whorls, grading from yellow-green with



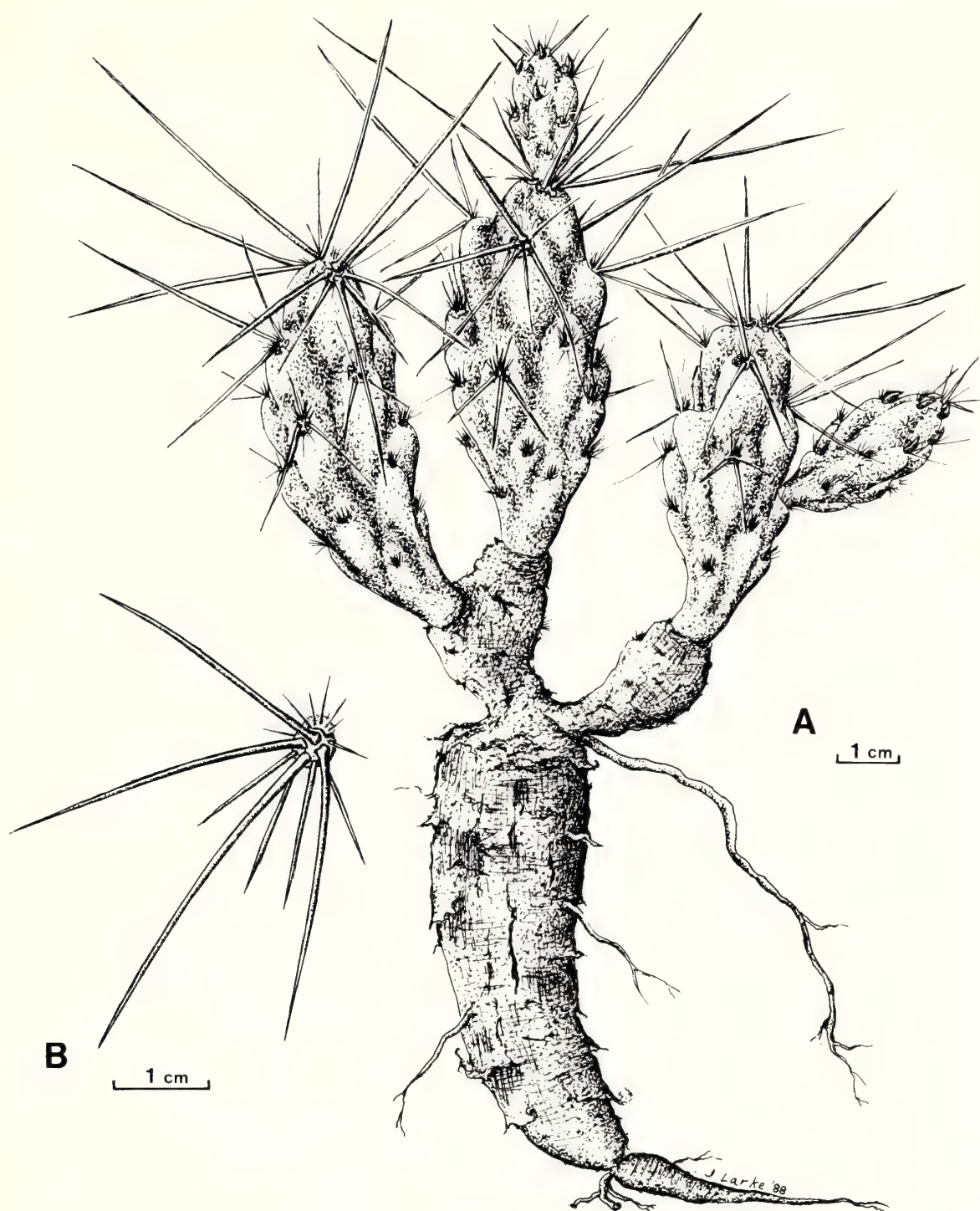


FIG. 2. *Opuntia aggeria* Ralston & Hilsenbeck. A. Habit showing tuberous root, characteristic branching pattern, and distribution of spine clusters. B. Detail of spine cluster. Illustrated from live specimen *Ralston 114*.

central pink tinge on the outer whorls to bright yellow in innermost series, to 25 mm long, 20 mm wide, spatulate, apiculate. Filaments green, to 8 mm long. Style cream, to 3 cm long. Pericarpel narrowly obconic, to 55 mm long, 20 mm wide with areoles bearing glochids. Fruits gray, dry at maturity, to 5 cm long. Seeds brown to cream, to 5 mm in diameter.  $n=11$ . Flowering late March to April.



*Paratypes.* USA, Texas, Brewster County, E of Nine-Point Mesa, 3 Aug 1948, *M. Anthony* 909 (MICH); 15 mi N of Terlingua, along road to Alpine, 14 Sep 1948, *M. Anthony* 1181 (MICH); flats just N of Santa Elena Canyon, BBNP, 15 Sep 1948, *M. Anthony* 1246 (MICH).

The specific epithet is chosen to describe the clumped or aggregated growth habit of this mound-forming species. Phenetically, *O. aggeria* appears most closely related to *O. grahamii* by its spine morphology, tuberous root system, and areole diameter, as well as to a species located in northern Mexico, *O. moelleri*. Comparison of *O. aggeria* to both *O. grahamii* and *O. moelleri* is given in Table 1. *Opuntia moelleri* is distributed in Coahuila, Mexico (Britton and Rose 1919; Bravo-Hollis 1978). Morphology (particularly the tuberous roots), geographic distribution, and the fact that *O. aggeria* and *O. moelleri* are the only known diploids in series *Clavatae*, suggest that these two species, through past hybridization, may be the progenitors of the more northerly distributed, tetraploid *O. grahamii*.

Chromosome counts from 12 populations of *O. aggeria* are all  $n=11$  (Table 2). If *O. aggeria* was the product of hybridization between *O. schottii* and *O. grahamii* as Anthony suggested, it would likely be a tetraploid, or if diploid, accompanied by possible hybrid sterility (cf. Ralston 1987). *Opuntia aggeria* is, however, highly fertile as determined by pollen stainability (Ralston and Hilsenbeck unpubl.) and, being a diploid, would be more or less reproductively isolated from the other two species of club cholla with which it co-occurs. Moreover, *O. aggeria* only occasionally exhibits characters intermediate between *O. grahamii* and *O. schottii*, whereas a true hybrid might be expected to show definite intermediacy, particularly a vegetatively propagated clonal entity as are many of the chollas, including *O. aggeria* (Grant 1981). The data thus show that the predominant club cholla occurring in BBNP (i.e., Anthony's putative hybrid) does not represent the product of hybridization between *O. schottii* and *O. grahamii* and should be formally recognized at the specific level.

2. *OPUNTIA GRAHAMII* Engelm., Proc. Amer. Acad. 3:304.—*Corynopuntia grahamii* (Engelm.) F. Knuth, Kactus ABC, 116 1935.—*Opuntia schottii* Engelm. var. *grahamii* (Engelm.) L. Benson, Cactus & Succ. J. (Los Angeles) 41:124. 1969.—*Gruersonia grahamii* (Engelm.) H. Robinson, Phytologia 26:176. 1973.—TYPE: USA, Texas, sandy soil in the bottom of the Rio Grande, near El Paso. 1851, *Wright Opuntia* no. 10 (lectotype, MO!).

Plants forming low sprawling mounds, 8 cm high, to 3 dm wide. Roots thickened, fleshy, tuberous. Branches creeping, with new



growth added apically, ascending; joints obovate, 3.5–5 cm long, 1.5–3 cm diameter; tubercles broad, not prominent, to 6 mm wide, 8–12 mm long, 4–6 mm high, green; areoles circular, 3–4 mm wide. Spines 7–14 per areole in upper half of joint. Spines mostly terete, straw-colored, with pink tinge; spine sheaths caducous, to 3 mm long; glochids numerous, increasing in number toward base of joint, to 5 mm long on old joints; 3–4 larger spines per areole, 1.5–5 cm long, spreading; 1–9 shorter spines, 5–25 mm long, spreading; 2–4 of these shorter spines deflexed. Flowers to 5 cm long, 4 cm wide; petaloids in 3–4 whorls grading from yellow with central pink tinge in outer ones to bright yellow in innermost series, to 20 mm long, 15–20 mm wide, spatulate, apiculate; filaments yellow green to 10 mm long; style cream, to 25 mm long; pericarpel obconic, 25–30 mm long and to 20 mm in diameter, with numerous glochids in areoles. Fruits and seeds unknown except in type illustration.  $n=22$ . Flowering early May through early June.

Many features distinguish *O. schottii* and *O. grahamii* (Table 1). Any intergradation through hybridization is now unlikely, as the ranges of the two species are marginally sympatric because of differing ecological preferences, and they differ in phenology as well.

3. *OPUNTIA SCHOTTII* Engelm., Proc. Amer. Acad. 3:304. 1856.—*Corynopuntia schottii* (Engelm.) F. Knuth. Kactus-ABC. 114. 1935.—*Grusonia schottii* (Engelm.) H. Robinson. Phytologia 26:176. 1973.—TYPE: USA, Texas, Rio Grande, near mouth of Pecos and San Pedro, Sep 1853, *A. Schott s.n.* (lectotype, MO!).

Plants forming extensive mats to 8 cm high, 5 m wide. Roots fibrous. Branches sprawling, forming long chains, new growth emerging from lateral areoles of previous year's growth; joints to 6.5 cm long, 3 cm diameter; tubercles prominent, 15–20 mm long, 6–8 mm wide, and 6–8 mm high, green; areoles circular, to 7 mm wide. Spines 8–14, flattened, reddish brown; spine sheaths to 5 mm long; 3–4 spines per areole 4–6 cm long, with 1 prominent central spine; 2–8 spines per areole shorter, to 30 mm long, spreading, 2–4 spines per areole deflexed; glochids not abundant, to 5 mm long. Flowers 5.5–6.5 cm long, to 3 cm wide; petaloids in 3–4 whorls grading from yellow green with central pink tinge in outer ones to bright yellow in innermost series, to 22 mm long, 10 mm wide, spatulate, apiculate; filaments yellow, to 10 mm long; style cream, to 25 mm long; stigma lobes 5–7, pink tinged; pericarpel narrowly obconic, to 30–45 mm long, 25 mm wide, with glochids in areoles. Fruits fleshy, yellow, to 45 mm long; areoles on fruits bearing spines and glochids to 5 mm long, fruits often persisting to following year. Seeds cream to brown, to 4 mm wide, with beaked aril.  $n=22$ . Flowering mid-June to early July.

*Opuntia schottii* appears most closely related, particularly through



its fibrous root system and flattened spine morphology, to *O. emoryi*, a species predominantly distributed in Arizona (however, see below). Morphology (Table 1), differing phenology, and its occupation of more mesic habitats primarily east of the Pecos River, easily distinguish *O. schottii* from the other species of club chollas in Trans-Pecos, Texas.

4. *OPUNTIA EMORYI* Engelm., Proc. Amer. Acad. 3:303. 1856.—*Cactus emoryi* Lemaire. Cactees 88. 1868.—*O. stanlyi* Engelm. [in Emory, Notes Mil. Recon., 157, fig. 9. 1848, nom. prov.] ex B. D. Jackson. Index Kewensis 2:358. 1895.—*Corynopuntia stanlyi* Knuth. Kactus-ABC. 114. 1935.—*Grunsonia stanlyi* (Engelm.) H. Robinson. Phytologia 26:176. 1973.—TYPE: Mexico, arid soil south and west of El Paso, especially between the sandhills and Lake Santa Maria, 1852, *Bigelow s.n.* (lectotype, MO!, seeds only).

Plants forming low sprawling mats to 15 cm high, 4 m wide. Roots fibrous. Branches forming chains; new growth emerging from areoles of previous year's growth. Joints 7–15 cm long, 5 cm in diameter; tubercles prominent, 35–50 mm long, 10–15 mm wide, 10–12 mm high, green; areoles circular to 7 mm wide. Spines 11–16, flattened yellow to red/brown; 6–8 spines 3.5–7 cm long, 5–8 spines 10–25 mm long. Glochids sparse to 5 mm long. Flowers 5.5–6.5 cm long, and to 3 cm wide; petaloids in 3–4 whorls grading from yellow green with central pink tinge outermost to bright yellow innermost, 25 mm long, 15 mm wide, spatulate, apiculate; filaments yellow, to 10 mm long; style cream, to 25 mm long; stigma lobes 5–7, pink tinged. Pericarpel narrowly obconic, 30–45 mm long, 20 mm wide, with areoles bearing glochids. Fruits and seeds not known for Texas population.  $n=22$ . Flowering May to early June.

In Texas, *O. emoryi* appears most closely related to *O. schottii*. Although *O. emoryi* is primarily known from Arizona, a disjunct population has been recently documented in the Big Bend region of West Texas near Candelaria in southern Presidio County (Weedin and Powell 1978; Ralston 1987; Ralston and Hilsenbeck in prep.). *Opuntia emoryi*, also a tetraploid species, is peripheral to the taxonomy of *O. aggeria* but is nonetheless an important, recent addition to the Texas flora. The larger size of the plants, including the much larger joints and tubercles, distinguishes *O. emoryi* from other species in the complex. Further study within the complex, however, and within series *Clavatae*, that takes into full account the northern Mexico and Arizona taxa is warranted.

#### ACKNOWLEDGMENTS

The authors wish to thank Drs. A. M. Powell, A. D. Zimmerman, and D. J. Pinkava for their helpful advice throughout this project. Ms. Julia Larke is thanked for the



illustration and Ms. Rena Gallego for technical assistance. Support for this study was provided by a Texas State Legislature Chihuahuan Desert Studies Grant #1141-30212-00 awarded to R.A.H.

#### LITERATURE CITED

- ANTHONY, M. 1956. The Opuntiae of the Big Bend region of Texas. *Amer. Midl. Naturalist* 55:225–256.
- BENSON, L. 1969. The cacti of the United States and Canada—new names and nomenclatural combinations—I. *Cactus & Succ. J.* 41:124–128.
- . 1982. The cacti of the United States and Canada. Stanford Univ. Press, Stanford, CA.
- BRAVO-HOLLIS, HELIA. 1978. Las cactaceas de México, 2nd ed. Universidad Nacional Autonoma de México, Ciudad Universitaria, México, DF.
- BRITTON, N. L. and J. N. ROSE. 1919. The Cactaceae, Vol. 1. Carnegie Inst. Wash. 248.
- ENGELMANN, G. 1856. Synopsis of the Cactaceae of the territory of the United States and adjacent regions. *Proc. Amer. Acad. Arts* 3:259–311.
- GRANT, V. 1981. Plant speciation, 2nd ed. Columbia Univ. Press, New York.
- PINKAVA, D. J. and B. D. PARFITT. 1982. Chromosome numbers in some cacti of western North America—IV. *Bull. Torrey Bot. Club* 109:121–128.
- , M. A. BAKER, B. D. PARFITT, and M. W. MOHLENBROCK. 1985. Chromosome numbers in some cacti of western North America—V. *Syst. Bot.* 10:471–483.
- RALSTON, B. E. 1987. A biosystematic study of the *Opuntia schottii* complex (Cactaceae) in Texas. M.S. thesis. Sul Ross State Univ.
- WEEDIN, J. F. and A. M. POWELL. 1978. Chromosome numbers in Chihuahuan Desert Cactaceae: Trans-Pecos Texas. *Amer. J. Bot.* 65:531–537.
- , ———, and D. O. KOLLE. 1989. Chromosome numbers in Chihuahuan Desert Cactaceae. II. Trans-Pecos Texas. *Southw. Naturalist* 34:160–164.
- WENIGER, D. 1984. Cacti of Texas. Univ. Texas Press, Austin.

(Received 18 Jan 1989; revision accepted 5 Jun 1989.)

## ANNOUNCEMENT

### NEW PUBLICATIONS

- CRAWFORD, R. M. M., *Studies in plant survival: Ecological case histories of plant adaptation to adversity*, Blackwell Scientific Publications, Osney Mead, Oxford OX2 0EL, 1989, x, 296 pp., illus., ISBNs 0-632-01475-X (hardbound), 0-632-01477-6 (paperbound), prices unknown. [= *Studies in Ecology*, Vol. 11. Discusses many plant examples for Arctic, montane, desert, coastal, and other areas.]
- CULLMANN, W., E. GÖTZ and G. GRÖNER, *The encyclopedia of cacti*, trans. by K. M. Thomas, Timber Press, 9999 SW. Wilshire, Portland, OR 97225, 1986 (publ. 1987), 340 pp., illus. (most color), endpaper maps, ISBN 0-88192-100-9 (hardbound), \$49.95. [Publ. in Britain by Alphabooks, Sherborne, same title, 1986. Translation of *Kakteen*, 2. Aufl., Eugen Ulmer GmbH & Co., 1984. With excellent photos, clear descriptions, and many keys to taxa.]



# BIOSYSTEMATIC STUDIES OF *PHACELIA CAPITATA* (HYDROPHYLLACEAE), A SPECIES ENDEMIC TO SERPENTINE SOILS IN SOUTHWESTERN OREGON

J. STEPHEN SHELLY<sup>1</sup>

Department of Botany and Plant Pathology,  
Oregon State University, Corvallis, OR 97331

## ABSTRACT

Studies of the distribution, edaphic restriction, cytology, and morphology of *Phacelia capitata* were undertaken to assess the relationship of the species within the *Phacelia magellanica* polyploid complex. *Phacelia capitata* is restricted to serpentine or related substrates in Coos, Douglas, and Jackson counties in southwestern Oregon. Chromosome counts of  $n=11$ , the base number for the complex, were obtained from 19 of 20 populations sampled. Two populations contained tetraploid ( $n=22$ ) individuals, one of these being a mixed population of diploids and tetraploids. Morphological studies uphold the distinctiveness of *P. capitata* at the diploid level. The origin of the tetraploids is problematic, but some specimens suggest that *P. capitata* has hybridized in the past with *P. heterophylla* ssp. *virgata* and plants resembling *P. hastata*. Owing to their scarcity and geographic restriction these hybridization events appear to have been recent, and they do not challenge the status of *P. capitata* as one of the most morphologically and ecologically distinct members of the *P. magellanica* complex. The species appears to be an example of an edaphic neoendemic.

Ultramafic soils are those derived from the igneous rocks peridotite and dunite and their metamorphic derivative, serpentinite. The spectacular influences that these substrates have on the plants that inhabit them are well known, and are of great interest to community ecologists and biosystematists. Serpentine vegetation is frequently dwarfed, and xerophytism is common. Species composition is often unique, and endemism and range disjunction are characteristic of serpentine floras (Kruckeberg 1969, 1984; Whittaker 1954, 1960).

In southwestern Oregon, serpentine substrates occur over large areas in Curry and Josephine counties, and in smaller and more widely scattered outcrops to the north and east in Coos, Douglas, and Jackson counties (Fig. 1). *Phacelia capitata* Kruckeberg is restricted to the northeasternmost serpentine outcrops in this region.

*Phacelia capitata* is a member of the *P. magellanica* (Lam.) Cov. polyploid complex, a wide-ranging group of biennial and perennial species having affinities with the South American species *P. secunda* Gmel. (= *P. magellanica*). The members of this polymorphic group

<sup>1</sup> Present address: Montana Natural Heritage Program, State Library, 1515 E. 6th Avenue, Helena, MT 59620.



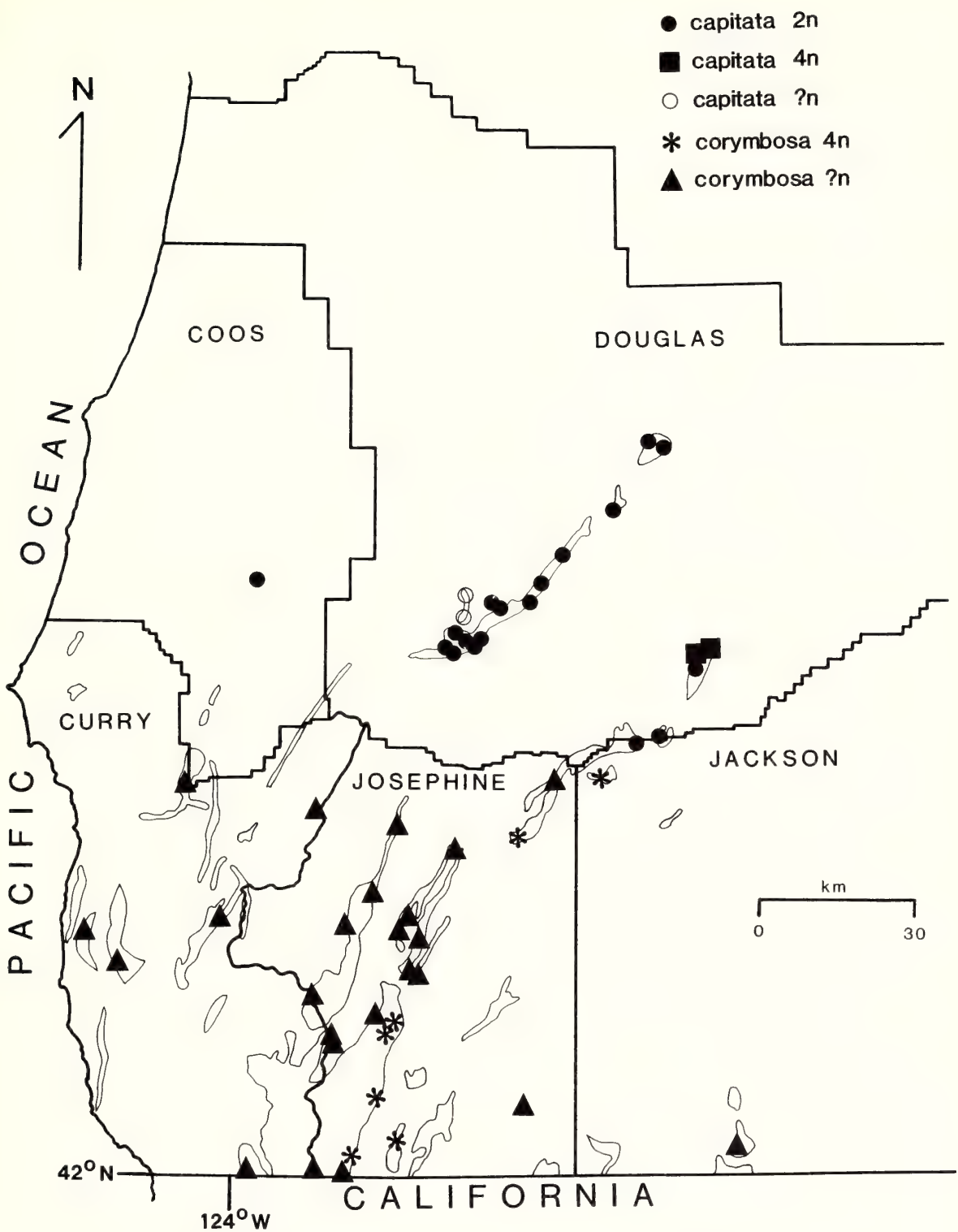


FIG. 1. Geographic distribution and chromosome numbers of *Phacelia capitata* and *P. corymbosa* in southwestern Oregon. Ultramafic formations are outlined (Wells and Peck 1961). *Phacelia corymbosa* locations are plotted from herbarium specimens housed at OSC, except for the tetraploid location at Sexton Mountain, Josephine County (Heckard 1960).

form a polyploid pillar complex (Stebbins 1971) that has a foundation comprising seven species with a base chromosome number of  $x=11$ , including *P. capitata* (Heckard 1960 and pers. comm.). The latter was described by Kruckeberg (1956). In his detailed study,



however, Heckard (1960) did not assess the interrelationships of *P. capitata* within the *P. magellanica* complex.

Owing to its restriction to serpentine soils (or closely similar derivatives) over a small geographic area, *P. capitata* has received attention as a potentially threatened species. Most recently it has been placed on the "watch list" of Oregon rare, threatened, and endangered plant species (Oregon Natural Heritage Data Base 1987). In addition, the species is a Category 2 federal candidate, under review for possible listing by the U.S. Fish and Wildlife Service (U.S. Department of Interior 1985).

My study was undertaken to assess the distribution, edaphic restriction, cytology, and morphological characteristics of *P. capitata*. I also studied natural populations of other species in the complex that occur in southwestern Oregon (*P. corymbosa* Jepson, *P. hastata* Douglas ex Lehmann, and *P. heterophylla* Pursh), to evaluate the interrelationships of *P. capitata* within the *P. magellanica* complex.

## METHODS

*Distribution.* I compiled locations for 13 *P. capitata* populations from specimens deposited at various herbaria (CAS/DS, HSC, JEPS, ORE, OSC, UC, and WTU), from the Oregon Rare, Threatened, and Endangered Plant files housed in OSC, from U.S. Bureau of Land Management offices in Roseburg and Medford, Oregon, and from the Oregon Natural Heritage Data Base in Portland. My field studies were conducted during May–July 1982, April 1983, and April–June 1984. I surveyed as many locations as possible, in both serpentine and non-serpentine areas of southwestern Oregon, to determine the location and status of *P. capitata* populations.

*Edaphic restriction.* To characterize the edaphic environment of the ultramafic areas occupied by *P. capitata*, I collected soil samples from four fully serpentinized locations, and from one less serpentinized site. In addition, I sampled two serpentine locations for *P. corymbosa*, and one non-serpentine location for *P. heterophylla*. The soil analyses were conducted by the Soil Testing Laboratory at Oregon State University, using the extraction and analysis methods of Berg and Gardner (1978).

*Cytology.* Chromosome counts were made from pollen mother cells. Immature helicoid cymes were field-fixed in a mixture of 3 parts 95% ethanol : 1 part glacial acetic acid (V:V) for 24 hours. They were then washed in two overnight changes of 70% ethanol, and frozen in a third change of the same. After warming at 55–60°C for 24–48 hours in an alcoholic hydrochloric acid-carmin stain (Snow 1963), the cymes were rinsed in distilled water and studied immediately, or stored in 70% ethanol in a freezer. Anthers were dissected



onto slides, squashed in 45% acetic acid, and semi-permanently mounted.

*Morphological studies.* A total of 530 living individuals from 26 natural populations in southwestern Oregon was studied. For *P. capitata*, 420 plants from 20 populations were examined. For comparison with *P. capitata*, 110 plants representing other members of the *P. magellanica* complex were studied: 80 of *P. corymbosa* (4 populations), 20 of *P. heterophylla* ssp. *virgata* (E. Greene) Heckard (1 population), and 10 of *P. hastata* (1 population).

Data for 10 morphological characteristics were collected from each plant studied: blade length (mm), leaf width (mm), width of corolla opening (mm), corolla length (mm), calyx length (mm), stem height (cm), number of leaf lobes, number of floral branches below the terminal cymes, type of leaf lobing, and glandulosity. The five leaf and flower characters were measured with a Zeiss 10× handlens containing a 10 mm scale. Stem height was measured from the base of the flowering stem to the tip of the terminal cymes. Qualitative assessments of the type of leaf lobing and the degree of glandulosity were made in the following manner:

*Type of leaf lobing*

0—leaves entire.

1—leaves pinnatifid (lobes with a broad base at the midvein).

2—leaves pinnately compound (lobes reaching the midvein, with entire leaflets distinguishable).

*Glandulosity* (when viewed with 40× Zeiss dissecting microscope)

0—eglandular.

1—a few scattered glandular trichomes among the longer tapering trichomes, mainly in and near the inflorescence.

2—densely and conspicuously glandular, especially on intermediate-length trichomes in and near the inflorescence, on the pedicels, and on calyces.

The mean values for each of the ten morphological characteristics were calculated for each population and subjected to a cluster analysis using CLUSTER, a hierarchical, agglomerative, combinatorial program (Keniston 1978). The Bray-Curtis dissimilarity index was used, and the data were standardized using division by the attribute maximum, in which all values for a given morphological attribute are divided by the maximum value observed for that attribute. This removes “high score bias,” and allows use of quantitative and qualitative values together. A group average fusion strategy was used; this method produces only moderately sharp clustering, but more directly reflects the relationships originally expressed by the dissimilarity measure (Boesch 1977).

I compared the stem vestiture of *P. capitata* with that of *P. cor-*



*ymbosa*, another serpentine member of the *P. magellanica* complex, using scanning electron microphotographs prepared by the Oregon State University Scanning Electron Microphotography Lab.

## RESULTS

*Distribution.* Twenty-two extant populations of *P. capitata* were located and studied (Table 1, Fig. 1). These populations are associated with the northeasternmost serpentine outcrops in southwestern Oregon, in central and southwestern Douglas, southern Coos, and northwestern Jackson counties (Fig. 1). The populations are generally located on slopes with southerly exposures, and occur at elevations from 100 to 1460 m.

Six populations of *P. corymbosa*, two of *P. heterophylla* ssp. *virgata*, and one of *P. hastata* were also studied (Table 1). At only one location was *P. capitata* found growing in biotic sympatry with any other member of the *P. magellanica* complex; at the Boomer Hill (west) site in Douglas County (the "sub-serpentine" location), it occurs along a disturbed road bank in a mixed population with the plants identified herein as *P. hastata*.

*Edaphic restriction.* Table 2 presents the results for eight soil analyses. Soils at the Boomer Hill (west) site (*P. capitata* and *P. hastata*) appear to be derived from metamorphic rocks similar to serpentine, but darker blackish-orange in color. The Tiller sample is from a non-serpentine area adjacent to the serpentine outcrops along Elk Creek in Douglas County. The remaining six samples are for soils derived from fully serpentinized parent materials; the rocks are a shiny, deep greenish-black color.

The serpentine soils are all characterized by low levels of phosphorus and low Ca/Mg ratios; these properties have been well-documented (Kruckeberg 1984; Proctor and Woodell 1975). The sub-serpentine sample has a higher Ca/Mg ratio than the more typical serpentine soils, but it is within the range of values reported by Proctor and Woodell (1975) for such soils.

Although large amounts of iron are often found in serpentine soils (Proctor and Woodell 1975), the results do not indicate this for the samples obtained in my study. The highest concentrations of iron are found in the sub-serpentine and non-serpentine samples.

The remaining analyses (pH, K, Cu) do not indicate any consistent differences between the serpentine and non-serpentine samples. Serpentine soils from the *P. capitata* and *P. corymbosa* sites are similar in chemical composition.

*Cytology.* At 19 of 20 sites, *P. capitata* occurs at the base (diploid) chromosome level of  $n=11$  (Table 1). Of particular interest are the Elk Creek and Callahan Creek populations, both of which contain



TABLE 1. STUDY POPULATIONS AND CHROMOSOME NUMBERS FOR THE *PHACELIA MAGELLANICA* COMPLEX, SOUTHWESTERN OREGON. All collection numbers are those of the author (JSS), except where noted. Voucher specimens are deposited in the Oregon State University Herbarium (OSC). Site names denote approximate locations; specific data are available from the author. An asterisk indicates a representative voucher from the same population, the actual chromosome count having been obtained from a separate, unvouchered individual.

---

|   |
|---|
| <i>P. capitata</i> Kruckeberg. $n=11$ —OR, Coos Co.: Bridge, <i>A. Kruckeberg</i> 2703 (WTU, isotype). Douglas Co.: Beatty Creek, 419; Bilger Creek, <i>JSS and M. Nelson</i> 724; Boomer Hill (W), <i>JSS and R. Holmes</i> 766; Boomer Hill (E), <i>JSS and R. Holmes</i> 781; Cow Creek (central), 405; Cow Creek (W), 411; Cow Creek (E), 681; Doe Creek, 706; The Drew, <i>JSS and M. Nelson</i> 734*; Elk Creek, <i>JSS and M. Nelson</i> 726; Lee Creek, 399; Little River, 690*; Myrtle Creek (N), 414; Peel, 354*; SW flank of Red Mountain, <i>JSS and M. Nelson</i> 736; Salt Creek, <i>JSS and M. Nelson</i> 725*; Weaver Road, 689. Jackson Co.: Goolaway Gap, <i>JSS and M. Nelson</i> 738. |
| <i>P. capitata</i> Kruckeberg. $n=22$ .—OR, Douglas Co.: Callahan Creek, 440; Elk Creek, <i>L. Heckard</i> 2930 (JEPS), <i>JSS</i> 433.   |
| <i>P. capitata</i> Kruckeberg. Chromosome number unknown—OR, Douglas Co.: Doe/Thompson Ridge, <i>JSS and R. Holmes</i> 783; Rice Creek, <i>JSS and R. Holmes</i> 792.   |
| <i>P. corymbosa</i> Jepson. $n=22$ —OR, Jackson Co.: Grave Creek, 441. Josephine Co.: Eight Dollar Mountain (S), 700; Eight Dollar Mountain (N), 702; Rough and Ready Creek, 698; Waldo, 697; Wimer Road, <i>L. Constance and R. Bacigalupi</i> 3394 (WTU).   |
| <i>P. hastata</i> Douglas ex Lehmann (see comments in Results section). $n=22$ —OR, Douglas Co.: Boomer Hill (W), <i>JSS and R. Holmes</i> 767.   |
| <i>P. heterophylla</i> Pursh ssp. <i>virgata</i> (E. Greene) Heckard. $n=11$ —OR, Douglas Co.: Cow Creek, 714; Elk Creek, <i>JSS and M. Nelson</i> 728.   |

---

tetraploid individuals; the Elk Creek population also contains diploids. Thus, all seven species in the *P. magellanica* complex that occur as basic diploids are now known to have morphological counterparts at the tetraploid ( $n=22$ ) level.

Two previous tetraploid counts for *P. corymbosa* in Oregon were cited by Heckard (1960). These, plus five additional counts obtained during this study, indicate that *P. corymbosa* may occur primarily at this level in Oregon. Diploids of this species are known to occur in the North Coast Ranges of California, and in one locality in the Sierra Nevada (Heckard 1960).

Three diploid counts for *P. heterophylla* in southwestern Oregon were previously recorded (Heckard 1960). The two additional counts reported here indicate that this species (as ssp. *virgata*) is primarily diploid in Oregon, although it occurs at the tetraploid level elsewhere in its range, mainly as ssp. *heterophylla* (Heckard 1960).

The tetraploid count reported here for *P. hastata* is apparently the first from southwestern Oregon. Although it was initially known only as a tetraploid, diploid individuals of this species have recently been discovered in northern Nevada (L. Heckard pers. comm.). It should be noted that the population identified throughout this paper



TABLE 2. SOIL ANALYSES FROM EIGHT *PHACELIA* SITES IN SOUTHWESTERN OREGON.

| Species and population | Soil type      | pH  | P<br>(ppm) | K<br>(ppm) | Ca<br>meq/100 g | Mg<br>meq/100 g | Ca/Mg<br>ratio | Cu<br>(ppm) | Fe<br>(ppm) |
|------------------------|----------------|-----|------------|------------|-----------------|-----------------|----------------|-------------|-------------|
| <i>P. capitata</i>     |                |     |            |            |                 |                 |                |             |             |
| Beatty Creek           | serpentine     | 7.1 | 4          | 35         | 2.1             | 12.3            | 0.17           | 1.1         | 74          |
| Boomer Hill (W)        | sub-serpentine | 6.2 | 19         | 82         | 17.6            | 7.7             | 2.3            | 1.8         | 124         |
| Bridge                 | serpentine     | 6.9 | 2          | 140        | 3.1             | 20.0            | 0.16           | 2.1         | 64          |
| Elk Creek              | serpentine     | 7.5 | 1          | 70         | 1.7             | 20.4            | 0.08           | 2.4         | 84          |
| Peel                   | serpentine     | 6.7 | 4          | 31         | 1.7             | 10.4            | 0.16           | 0.76        | 86          |
| <i>P. corymbosa</i>    |                |     |            |            |                 |                 |                |             |             |
| Eight Dollar Mtn (N)   | serpentine     | 6.9 | 1          | 39         | 2.5             | 23.3            | 0.11           | 1.7         | 94          |
| Grave Creek            | serpentine     | 7.2 | 1          | 39         | 2.0             | 11.5            | 0.17           | 1.1         | 40          |
| <i>P. heterophylla</i> |                |     |            |            |                 |                 |                |             |             |
| Tiller (Elk Creek)     | non-serpentine | 6.8 | 34         | 43         | 6.3             | 1.2             | 5.25           | 1.5         | 142         |



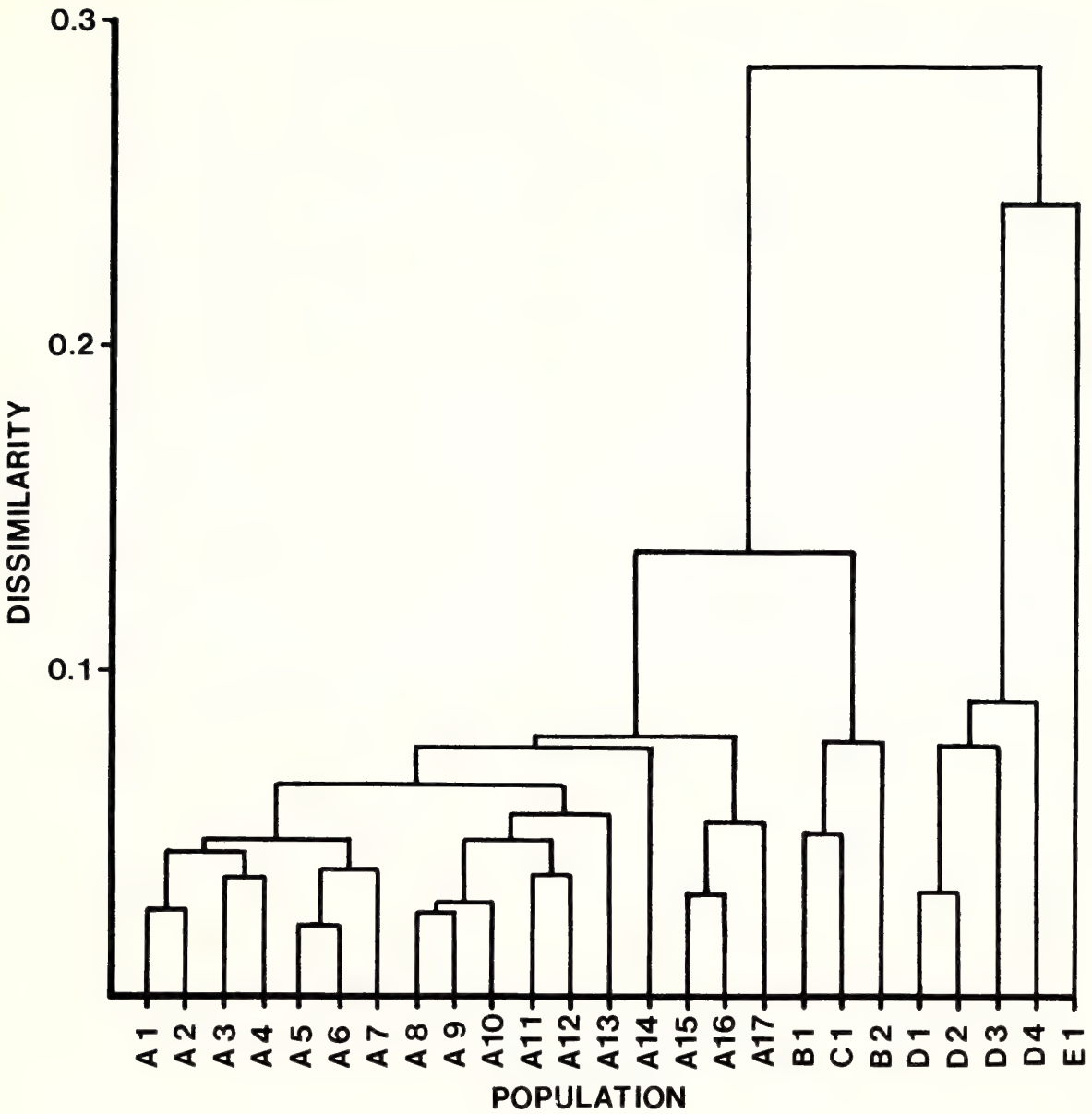


FIG. 2. Cluster analysis of *Phacelia* populations in southwestern Oregon. A = *P. capitata* (2n); B = *P. capitata* (4n); C = *P. hastata* (4n); D = *P. corymbosa* (4n); E = *P. heterophylla* ssp. *virgata* (2n).

as *P. hastata* would represent a range extension for a species whose main distributional range otherwise lies entirely east of the Cascade-Sierra crest (Heckard 1960). It is possible that the parentage of these plants may involve other members of the *P. magellanica* complex, including *P. egena* (L. Heckard pers. comm.). Thus, their identification as *P. hastata* remains speculative at this time.

*Morphological studies.* The results of the cluster analysis reveal four distinct groups of interest, at a dissimilarity level = 0.12 (Fig. 2). From left to right, these are: 1) diploid *P. capitata* (17 populations); 2) two *P. capitata* populations containing tetraploids, plus the plants suggestive of *P. hastata* (one population); 3) *P. corymbosa* (four populations); and 4) *P. heterophylla* ssp. *virgata* (one population).



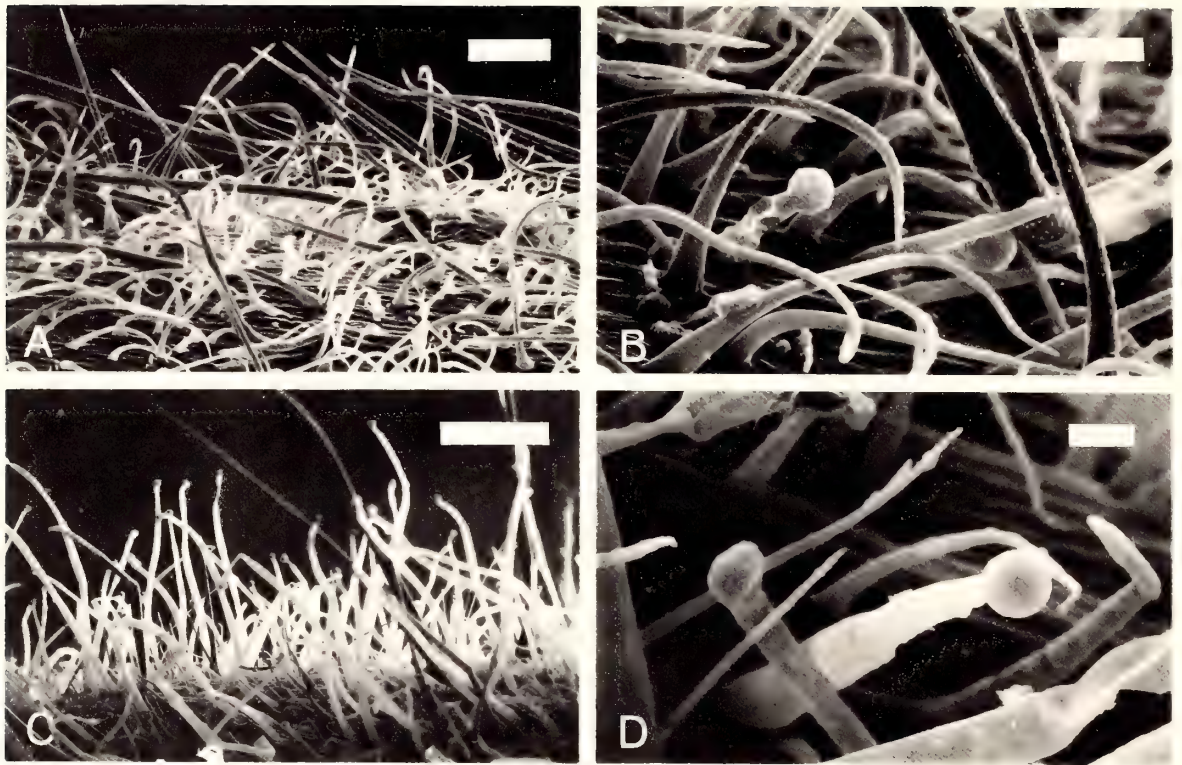


FIG. 3. SEM microphotographs of stem vestiture of *Phacelia capitata* and *P. corymbosa*, taken just below the terminal cyme branches. A, *P. capitata* stem vestiture (scale bar = 100  $\mu$ m); B, short glandular trichome of *P. capitata* (scale bar = 25  $\mu$ m); C, *P. corymbosa* stem vestiture (scale bar = 500  $\mu$ m); D, short glandular trichomes of *P. corymbosa* (scale bar = 25  $\mu$ m).

Photographs of stem vestiture, taken just below the terminal cyme branches, illustrate the conspicuous medium-length glandular trichomes of *P. corymbosa* (Fig. 3C), which are very important in distinguishing it from *P. capitata* (Fig. 3A). However, *P. capitata* is not eglandular (Fig. 3B) as described by Kruckeberg (1956), but possesses very small glandular trichomes similar to those of *P. corymbosa* (Fig. 3D).

A revised comparison of *P. capitata* with other members of the *P. magellanica* complex in southwestern Oregon is presented in Table 3. A revised description of *P. capitata*, modified from that of Kruckeberg (1956), is presented below.

*PHACELIA CAPITATA* Kruckeberg, Madroño 13:209. 1956.

Plants deeply taprooted caespitose perennials with 1-many thin, wiry flowering stems each arising from a rosulate tuft of leaves, with numerous sterile leaf rosettes often present. Stems erect, unbranched or occasionally branched, (11-)20-45(-63) cm tall. Herbage finely sericeous, the silvery-gray vestiture consisting of three trichome types: appressed bristles ca. 1-1.5 mm long, underlain by shorter, matted trichomes ca. 0.4-0.5 mm long, and scattered, very short glandular



trichomes, ca. 0.03–0.05 mm long, especially near the inflorescence, on the pedicels, calyx lobes, and leaf veins; long bristles sparse or absent on the lower portion of the stem. Sterile leaves (those in rosettes not subtending flowering stems) linear-lanceolate, simple and entire, very rarely pinnatifid or pinnately compound with 1–2 pairs of basal lobes, (1.7–)2.5–6.5(–8.8) cm long, (2.3–)2.9–6.0 (–13.0) mm wide, tapering to petioles 1–2 cm long; climax leaves (those in rosettes at the bases of flowering stems) entire, or occasionally having 1–2 basal lobe pairs; cauline leaves gradually but not wholly reduced upwards. Inflorescences of 2–3 helicoid cymes borne in a congested, capitate or subcapitate cluster, or frequently with 2 or more lateral cyme branches below the terminal cymes; pedicels in early fruit 1–3 mm long, hispid. Calyx lobes linear-oblong, (3.0–)4.2–6.6(–7.7) mm long, 0.5–0.8 mm wide, with long-hispid margins, the abaxial surface short-hirsute. Corollas white, rotate, cylindric, or occasionally slightly campanulate-spreading, (4.1–)5.0–6.9(–8.0) mm long, (2.3–)3.0–6.0(–8.4) mm broad when fresh, with entire, obtuse-rounded lobes; appendages attached barely a millimeter above the base of the corolla tube, the free portions forming a long (3 mm) and narrow “V” distally; stamens and style exerted 5–7 mm, the filaments glabrous or with a few scattered hairs about mid-length along the filament. Immature capsules ovoid, 2–3 mm long, densely clothed with stout bristles 2 mm long. Mature seeds 1.9–3.0 mm long (in diploid specimens), brown, with reticulate-pitted surface;  $n=11$ , 22.

#### DISCUSSION

The *Phacelia magellanica* alliance is an example of a mature polyploid complex. In such complexes, both the morphological and ecological extremes are usually represented by the diploid species. However, the diploids are often less common than the polyploids; their ranges are more restricted, and the amount of genetic variation within their populations is usually less. In addition, the diploids are usually allopatric, or sympatric only in restricted areas, so that the likelihood of hybridization and doubling of chromosome number is much reduced (Stebbins 1971).

In the *P. magellanica* complex, superimposed on a series of seven diploid ( $n=11$ ) species is an interfertile complex of tetraploids ( $n=22$ ) and a few hexaploids ( $n=33$ ). At the time of his study, Heckard (1960, p. 33) stated that each of the basic diploid species, except *P. capitata*, has a “. . . morphologically similar counterpart on the tetraploid level which intimately associates it with the superstructure of intergrading tetraploids.” This group is now known to include *P. capitata*. Heckard (1960) emphasized that the intergradation between polymorphic tetraploid species, often accom-



TABLE 3. COMPARISON OF *PHACELIA CAPITATA*, *P. CORYMBOSA*, *P. HASTATA*, AND *P. HETEROPHYLLA* SSP. *VIRGATA* IN SOUTHWESTERN OREGON.

| Species                                    | Chromosome<br>number ( <i>n</i> ) | Habit  | Stem height<br>(cm) | Leaf size   |            |
|--|-----------------------------------|--|---------------------|-------------|------------|
|  |                                   |  |                     | Length (cm) | Width (mm) |
| <i>P. capitata</i>                         | 11, 22                            | perennial, mat-forming   | 20-45               | 2.5-6.5     | 2.9-6.0    |
| <i>P. corymbosa</i>                        | 22                                | perennial, mat-forming   | 7.5-25              | 2.4-5.2     | 6.0-14.0   |
| <i>P. hastata</i>                          | 22                                | perennial, with 1-many stems, rarely<br>mat-forming in this region | 20-50               | 3.5-7.5     | 7.0-13.0   |
| <i>P. heterophylla</i> ssp. <i>virgata</i> | 11                                | biennial   | 30-75               | 3.8-8.0     | 8.0-17.0   |



TABLE 3. CONTINUED.

| Leaf outline  | Inflorescence   | Corolla shape                          | Glandulosity  |
|---|---|--|---|
| linear-lanceolate, entire; rarely, with 1-2 pairs of leaflets at base of lamina       | cymes often terminal or subterminal, or with 1-many lateral inflorescences below the terminal cymes | cylindric (campanulate in tetraploids) | scattered, very short glandular trichomes, especially near the inflorescences, on the pedicels, calyx lobes, and leaf veins |
| linear to lance-oblong, entire, or often with 1-2 pairs of leaflets at base of lamina | cymes terminal, or often with 1-2 subterminal cyme branches   | cylindric-campanulate                  | conspicuously glandular overall, with short-medium glandular trichomes  |
| lanceolate, entire, or rarely with 1-3 leaflets                                       | cymes terminal or subterminal, often with 1-many lateral inflorescences below the terminal cymes    | cylindric-campanulate                  | scattered, short glandular trichomes, especially near the inflorescences, on the pedicels, calyx lobes, and leaf veins      |
| pinnately dissected, with 1-4 pairs of lobes  | virgate, with 10-many overlapping lateral cymes   | cylindric-slightly flaring             | medium-length glandular trichomes frequent in the upper portions of the inflorescence                                       |



panied by introgression, has led to very complicated, and sometimes indecipherable, patterns of variation in the *P. magellanica* complex. This is especially true, he states (Heckard 1960, p. 33), because "... the initial differences are not of a magnitude to furnish characters which can be conveniently measured. The result of this intergradation is an extensive assemblage of interrelated plants within which lines must be drawn somewhat arbitrarily in order to delimit taxonomic units."

Of the seven species in the *P. magellanica* complex that occur predominantly or partially as diploids, two were considered in detail in this study: *P. capitata* and *P. corymbosa*. Each of these is a good example of a "morphological and ecological extreme," having very distinct morphological characteristics and special ecological attributes in the form of virtually complete restriction to serpentine soils. However, of all seven species that are now known to occur at both the diploid and tetraploid levels in the *P. magellanica* complex, *P. capitata* has the most restricted geographical range.

*Phacelia capitata* was found growing sympatrically with other members of the *P. magellanica* complex at only two locations. The only instance of biotic sympatry with another member of the group was found at the Boomer Hill (west) site, where, as described above, it occurs along a roadbank in a mixed population with the plants resembling *P. hastata*. Chromosome counts from this site showed that *P. capitata* occurs as a diploid and that the *P. hastata*-like plants are tetraploids, a situation that ordinarily limits the formation of fertile interspecific hybrids. Some collections (i.e., Shelly and Holmes 768, 771, OSC) are intermediate, however, in their possession of relatively narrow, predominantly entire, silvery leaves. Attempted chromosome counts for these intermediate plants were unsuccessful, as all the buds were past meiosis. On the basis of their morphological intermediacy, however, it appears that hybridization occurred in the past. Of interest at this site is the less stringent nature of the soil, which is intermediate between the highly serpentinized habitats to which *P. capitata* is otherwise restricted, and a non-serpentine soil profile. This, plus the disturbed nature of the roadside habitat, are possibly the factors which allowed *P. capitata* and the *P. hastata*-like plants to become sympatric here.

The Elk Creek population of *P. capitata*, containing diploids and tetraploids, further exemplifies the problems involved in determining the origins of hybrid individuals in the *P. magellanica* complex. On the basis of field observations, the most likely other diploid species involved in this intergradient population is *P. heterophylla*. This species is neighboringly sympatric with *P. capitata*, occurring on non-serpentine soils along the highway both north and south of the serpentine outcrops above Elk Creek. Surveys throughout the



area did not reveal any other morphologically distinct members of the *P. magellanica* complex. Numerous *P. capitata* plants at both Elk Creek and the nearby Callahan Creek site are morphologically suggestive of past hybridization with *P. heterophylla*, particularly in the possession of pinnately compound leaves, which are characteristic of the latter species.

The cluster analysis upholds the morphological distinctiveness of diploid populations of *P. capitata* in comparison with *P. corymbosa* ( $4n$ ), *P. hastata* ( $4n$ ), and *P. heterophylla* ( $2n$ ). The clustering of the two tetraploid *P. capitata* populations with the tetraploids resembling *P. hastata* is most likely due to similar tendencies toward longer, entire leaves, larger corollas, similar stem height, and an intermediate degree of glandulosity amongst the individuals.

Despite the evidence for past genetic interaction of *P. capitata* with *P. heterophylla* and with plants resembling *P. hastata*, it is appropriate to interpret these instances of limited interspecific gene exchange as exceptional events. *Phacelia capitata* remains a unique entity in the *P. magellanica* complex, as evidenced by the morphological, ecological, and almost wholly diploid cytological distinctiveness of the species.

Although the exact evolutionary history of *P. capitata* remains unknown, it seems most appropriate to categorize it as a serpentine neoendemic species. Such species are newly arisen "insular" taxa, often demonstrating a pattern of adaptive radiation into specialized habitats (Kruckeberg 1984). Additionally, because *P. capitata* would have evolved at the diploid level within the *P. magellanica* complex, it conforms well to the diploid speciation model for the establishment of an edaphic endemic species as described by Kruckeberg (1986). In this scheme non-serpentine populations, which may be preadapted for serpentine tolerance, give rise via disruptive selection and subsequent genetic divergence and isolation to new biological species.

The extent to which this process involved a diploid ancestor shared with *P. corymbosa*, if any, is enigmatic. In fact, no very close relative of *P. capitata* is apparent within the *P. magellanica* complex. No evidence of genetic interaction between *P. capitata* and *P. corymbosa* was found, despite their virtually complete restriction to similar serpentine substrates. The two species were found to be fully allopatric, *P. capitata* replacing *P. corymbosa* on the northeasternmost ultramafic outcrops in southwestern Oregon. In addition, *P. corymbosa* is not known to occur as a diploid in Oregon. The northernmost known diploid location for *P. corymbosa* is in Siskiyou County, California, approximately 175 km south of the southernmost location of *P. capitata* (Heckard 1960). Lastly, the two species are both distinct morphological entities in the *P. magellanica* com-



plex, and are very different from one another. If a common diploid ancestor was shared by the two species, it appears to have long been extinct.

Field studies revealed that in many places *P. capitata* has increased in abundance following habitat disturbance. Owing to this ruderal response, the species is not currently threatened or endangered with extinction. It is still important, however, to protect undisturbed populations of such narrowly endemic species so that features of their population ecology, habitat requirements, and evolutionary uniqueness may be studied in natural environments.

#### ACKNOWLEDGMENTS

This study was completed in partial fulfillment of the requirements for the degree of Master of Science, Oregon State University. I thank Kenton Chambers for his guidance. Support, research, and travel funds were provided by the Department of Botany and Plant Pathology and the Oregon State University Herbarium. Field assistance from Mark Nelson and Russ Holmes, and helpful advice from Robert Meinke, is gratefully acknowledged. LaRea Johnston assisted in the preparation of the photographs. Ginger King provided invaluable assistance in the preparation of the figures. I thank the Editor, L. R. Heckard, A. R. Kruckeberg, and an anonymous reviewer for helpful comments on the manuscript.

#### LITERATURE CITED

- BERG, M. G. and E. H. GARDNER. 1978. Methods of soil analysis used in the Soil Testing Laboratory at Oregon State University. Agricultural Experiment Station, Corvallis. Special Report No. 321.
- BOESCH, D. F. 1977. Application of numerical classification in ecological investigations of water pollution. U.S. Environmental Protection Agency, Corvallis, Oregon. Ecological Research Series Report No. EPA-600/3-77-033.
- HECKARD, L. R. 1960. Taxonomic studies in the *Phacelia magellanica* polyploid complex. Univ. Calif. Publ. Bot. 32:1-126.
- KENISTON, J. A. 1978. Program CLUSTER: an aid to numerical classification. Oregon State University, Marine Science Center, Newport (unpubl.).
- KRUCKEBERG, A. R. 1956. Notes on the *Phacelia magellanica* complex in the Pacific Northwest. Madroño 13:209-221.
- . 1969. Plant life on serpentinite and other ferromagnesian rocks in northwestern North America. Syesis 2:15-114.
- . 1984. California serpentines: flora, vegetation, geology, soils, and management problems. Univ. California Press, Berkeley.
- . 1986. An essay: the stimulus of unusual geologies for plant speciation. Syst. Bot. 11:455-463.
- OREGON NATURAL HERITAGE DATA BASE. 1987. Rare, threatened, and endangered plants and animals of Oregon. The Nature Conservancy, Portland.
- PROCTOR, J. and S. R. J. WOODDELL. 1975. The ecology of serpentine soils. Adv. Ecol. Res. 9:255-366.
- SNOW, R. 1963. Alcoholic hydrochloric acid-carmin as a stain for chromosomes in squash preparations. Stain Tech. 38:9-13.
- STEBBINS, G. L. 1971. Chromosomal evolution in higher plants. Edward Arnold Ltd., London.
- U.S. DEPARTMENT OF INTERIOR. 1985. Endangered and threatened wildlife and plants; review of plant taxa for listing as endangered or threatened species; notice of review. Federal Register 50:39525-39584.



- WELLS, F. G. and D. L. PECK. 1961. Geologic map of Oregon west of the 121st meridian. U.S. Geol. Survey Misc. Geol. Inv. Map I-325.
- WHITTAKER, R. H. 1954. The ecology of serpentine soils. IV. The vegetational response to serpentine soils. *Ecology* 35:275-288.
- . 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecol. Monogr.* 30:279-338.

(Received 8 Aug 1988; revision accepted 28 Jun 1989.)

## ANNOUNCEMENT

### SECOND ANNUAL CONFERENCE

#### THE SOCIETY FOR ECOLOGICAL RESTORATION

The Society for Ecological Restoration announces its second annual conference, to be held at the Sheraton International Hotel, at O'Hare, in Chicago, 29 April-3 May 1990. The program will include several special sessions to explore the state of the art as it applies to key environmental issues, and a full program of contributed papers and posters, special lectures, workshops, field trips, and other special events designed to facilitate communication among restorationists and with decision makers and the general public.

Special programs will include: Prairie Restoration, Restoration and Global Climate Change, Setting Standards for Monitoring Restoration Projects, Restoration and Recovery of Endangered Species, and Restoration Philosophy. Field trips will include visits to the prairie restoration project at Fermi National Laboratory, the Des Plaines River and wetland restoration project, Indiana Dunes National Lakeshore projects, Chicago's urban prairies, and the University of Wisconsin Arboretum and Society offices in Madison.

The Society invites submission of abstracts of papers dealing with all aspects of ecological restoration. Special consideration will be given to papers directly related to the special sessions listed above, but papers dealing with any aspect of ecological restoration are welcome. These may include political, administrative, social, economic, and philosophical, as well as purely scientific and technical aspects. Forms for submission of abstracts may be obtained from the Society's office: S.E.R., 1207 Seminole Highway, Madison, WI 53711, (608) 263-7889. The deadline for submission of Abstracts for Contributed Papers is 15 January 1990.



A SYSTEMATIC AND PHYTOGEOGRAPHIC STUDY OF  
*ANTENNARIA AROMATICA* AND *A. DENSIFOLIA*  
(ASTERACEAE: INULEAE) IN THE WESTERN  
NORTH AMERICAN CORDILLERA

RANDALL J. BAYER

University of Alberta, Department of Botany,  
Edmonton, Alberta T6G 2E9, Canada

ABSTRACT

*Antennaria aromatica* and *A. densifolia* are closely related species occurring in disjunct, unglaciated regions of the Rocky Mountain cordilleran system. The species are morphologically distinct and are readily distinguished based on a number of characters. They both occur on predominantly limestone talus slopes from subalpine to alpine elevations. Indications from the current distribution of the taxa and the known extent of glaciation suggest that they once had more extensive ranges and that these were subsequently reduced by the Wisconsinan glaciation. Glaciation has played a major role in the phytogeographic history of the species, as well as in their evolutionary divergence. A population of *A. densifolia* from Montana, disjunct from the main group of populations in the Northwest Territories and Yukon, is a noteworthy collection.

*Antennaria aromatica* Evert and *A. densifolia* A. Pors. are two narrowly restricted endemics of the Alpinae, a group of arctic/alpine *Antennaria* centered in western North America. Both occur on talus, primarily of limestone origin, but in different regions of the western North American cordillera. *Antennaria densifolia*, first described from the MacKenzie Mountains of the Northwest Territories, is apparently most common on the east slope of the MacKenzie Mountains and in the Ogilvie Mountains and southern Richardson Mountains of the Northwest Territories and Yukon Territory. Evert (1984) recently described *A. aromatica* from the Rockies of Montana and Wyoming (type from the Beartooth Pass near Quad Creek, Montana). Examination of herbarium material and the meager literature indicates that the morphological, ecological and distributional aspects of these two species are not well understood. Distributions of the species indicate that they once may have been more widespread and that their phytogeographic history, as well as their evolutionary divergence, was influenced greatly by Pleistocene glaciation. Comparison of specimens of both species indicates a close morphological similarity. Recently, a single disjunct population of *A. densifolia* has been discovered in a remote area of Montana. This, coupled with the ostensible morphological and ecological similarity of the two species, makes a detailed analysis of them appropriate.



TABLE 1. LIST OF 36 CHARACTERS AND CHARACTER STATES USED IN THE MORPHOMETRIC ANALYSIS OF *ANTENNARIA AROMATICA* AND *A. DENSIFOLIA*. Numbers following each character indicate the scale used. All qualitative state determinations are in mm.

---

|                                       |   |
|---------------------------------------|---|
| Basal rosette characters:             | 1. Length of entire basal leaf. 2. Maximum width of the basal leaves. 3. Length, along the mid-vein, from leaf tip to the maximum width. 4. Shape of the anterior margin, i.e., length from tip to widest point in the leaf. 5. Number of leaves per basal rosette.   |
| Stolon characters:                    | 6. Number of leaves per stolon. 7. Length of the largest leaf. 8. Width of the largest leaf. 9. Length of the smallest leaf. 10. Width of the smallest leaf. 11. Stolon length. 12. Number of stolons per basal rosette.  |
| Cauline (flowering) stem characters:  | 13. Flowering stem height. 14. Number of leaf nodes per cauline stem. 15. Width of the longest leaf. 16. Length of the longest leaf. 17. Width of the shortest leaf. 18. Length of the shortest leaf. 19. Presence of a scarious flag-like structure at the apex of the upper leaves, 0.0 = absent, 1.0 = present.  |
| Pistillate capitulescence characters: | 20. Height of the involucre. 21. Number of heads per capitulescence. 22. Phyllary length. 23. Phyllary width. 24. Corolla length. 25. Pappus length. 26. Achene length. 27. Phyllary colors, 1.0 = green base, white tips, 2.0 = green base, rose middle, white tips, 3.0 = green base, black/brown middle, white tips, 4.0 = green base, brown middle, rose tips, 5.0 = green base, brownish tips, 6.0 = brown base, white tips, 7.0 = brown base, rose tips, 8.0 = brown base, umber tips, 9.0 = brown base, dark brown tips, 10.0 = brown base, black or very dark green tips. 28. Number of florets per head. |
| Staminate capitulescence characters:  | 29. Height of the involucre. 30. Number of heads per capitulescence. 31. Phyllary length. 32. Phyllary width. 33. Corolla length. 34. Pappus length.  |
| Miscellaneous characters:             | 35. Presence of stalked glands on the surfaces of stems, leaves, etc., 0.0 = absent, 1.0 = present. 36. Presence of staminate individuals in the population, 0.0 = staminate absent (i.e., population all pistillate), 1.0 staminate present.   |

---

## METHODS

Specimens deposited at ALA, ALTA, CAN, DAO, ID, MONTU, RM, and UAC were examined for the morphological and phyto-geographic information. Chromosome counts were obtained from several collections of *A. aromatica* and one of *A. densifolia* utilizing the Feulgen chromosome staining methods described in Bayer (1984).

A principal components analysis (PCA) was used to quantify the morphological differences between the species. Forty specimens representing the range of morphological diversity from throughout the known range of each species were selected for morphometric analysis. Thirty-six vegetative and reproductive features (Table 1) were measured on twenty specimens of each taxon. In most cases specimens, having both staminate and pistillate individuals, were used, but complete specimens could not always be included because of the scarcity of good material. The original data matrix is available from the author upon request.

The NTSYS-pc program (Numerical taxonomy and multivariate analysis systems for the IBM-PC microcomputer and compatibles;



vers. 1.2; F. James Rohlf 1987) was used to compute the PCA. The STAND subroutine was used to standardize the data such that each character had a mean of zero and a standard deviation of unity. A similarity matrix of product-moment correlations was derived using the SIMINT subroutine of NTSYS-pc. The EIGEN subroutine was employed to compute the eigenvalue and eigenvector matrices. Three factors were extracted by the EIGEN subroutine. The OTU's were subsequently projected onto axes (the eigenvectors) using the PROJ subroutine of NTSYS-pc, thus concluding the principal components analysis. A 3-dimensional graph of the OTU's onto the first three principal components was plotted using the MOD3DG subroutine of NTSYS-pc.

## RESULTS

*Distribution and cytology.* The distribution of all available herbarium records for both taxa is presented in Figure 1. Additionally, the distribution of herbarium records having staminate, as well as pistillate specimens, and those having only pistillate specimens, is indicated. Although absence of staminate plants, as determined from gender ratios in natural populations, is a dependable indicator that the plants in the population are gametophytic apomicts (Bayer and Stebbins 1983), the lack of staminate plants on herbarium specimens provides only weak evidence because it could be a consequence of the failure of the collector to gather both genders in a particular population.

The base chromosome number in *Antennaria* is  $x=14$ . The only previous chromosome report (diploid) for *A. densifolia* is a Yukon population (Chmielewski and Chinnappa 1988). One population of *A. densifolia* from Montana has been determined as diploid (Table 2). Three populations of *A. aromatica* have been counted as diploid, whereas seven are tetraploid (Fig. 2, Table 2). One population of *A. aromatica* from the Big Horn Mountains has been counted as hexaploid, or  $2n=84$  (Fig. 2, Table 2), which is a new number for the species. The three diploid populations of *A. aromatica*, including the type locality, are from the southern part of the species range (Fig. 2). The tetraploid populations are more widespread, occurring from

→

FIG. 1. Distribution of *Antennaria aromatica* (circles) and *A. densifolia* (squares) in western North America (each symbol may depict one or more collections). Open symbols indicate collections containing pistillate and/or staminate individuals, while closed symbols signify collections having only pistillate plants. The continental divide is indicated by the dot/dash line and the Wisconsinan glacial maximum, following Prest (1984), is shown by "T" shaped symbols. Bar = 500 km.



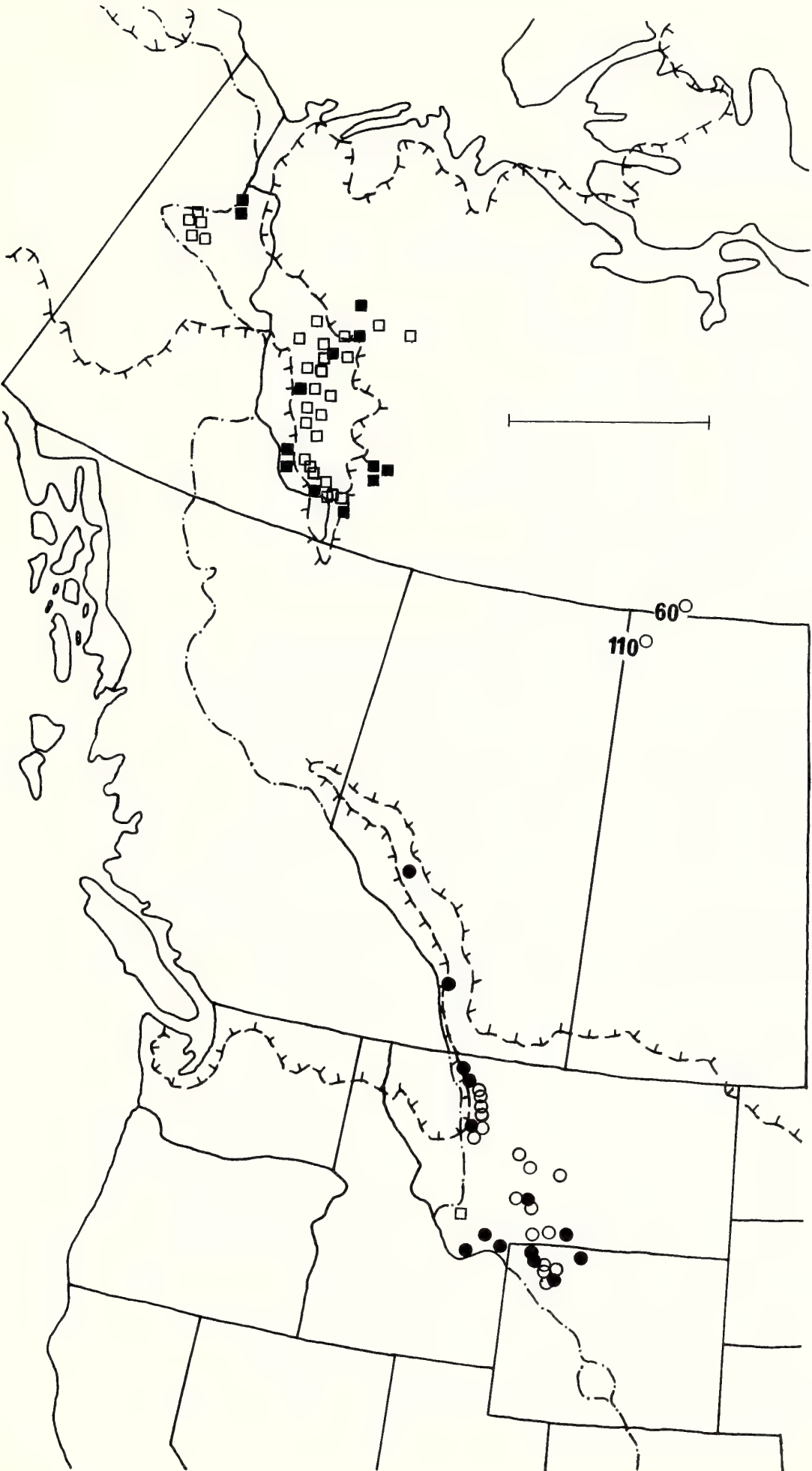




TABLE 2. SYNOPSIS OF CHROMOSOME NUMBERS FOR ELEVEN POPULATIONS OF *ANTENNARIA AROMATICA* AND TWO POPULATIONS OF *A. DENSIFOLIA*. Presented are state/province, county or mountain range, and voucher number. Report reference codes: a = current study (vouchers at ALTA), b = Bayer (1984), c = Bayer and Stebbins (1987), and d = Chmeilewski and Chinnappa (1988). \* = new number for the species. \*\* = population presumably asexual, containing only pistillate individuals.

| State or province      | County or mountain range | Voucher number | Somatic number | Reference codes |
|------------------------|--------------------------|----------------|----------------|-----------------|
| <i>A. aromatica</i> :  |                          |                |                |                 |
| Montana                | Carbon Co.               | 8092           | 28             | b               |
| Montana                | Gallatin Co.             | MT-628         | 28             | a               |
| Wyoming                | Park Co.                 | WY-836         | 28             | a               |
| Montana                | Cascade Co.              | MT-747         | 56             | a               |
| Montana                | Gallatin Co.             | 8105**         | 56             | b               |
| Montana                | Judith Basin Co.         | MT-754         | 56             | a               |
| Montana                | Lewis and Clark Co.      | MT-890         | 56             | a               |
| Montana                | Madison Co.              | MT-634**       | 56             | a               |
| Montana                | Teton Co.                | M-302          | 56             | c               |
| Wyoming                | Park Co.                 | WY-626**       | 56             | a               |
| Wyoming                | Big Horn Co.             | WY-813**       | 84*            | a               |
| <i>A. densifolia</i> : |                          |                |                |                 |
| Montana                | Granite Co.              | MT-725         | 28             | a               |
| Yukon                  | Ogilvie Mtns.            | 2642/2643      | 28             | d               |

the northern part of the range in Teton Co., Montana south to Madison Co., Montana and Park Co., Wyoming (Fig. 2).

*Morphometrics.* The 3-dimensional graph displaying the first three factors from the principal components analysis (PCA) is presented as Figure 3. The first three axes account for 57.06% of the variation and the first 10 factors have individual eigenvalues greater than 1.000, indicating that the variables are not highly correlated. Factor 1 has highest loadings for the characters of presence/absence of glands (Table 1; character 35), pistillate phyllary length (character 22); and various leaf length characters (characters 1, 7, and 9). Stolon length (character 11), number of stolons/basal rosette (character 12), and the presence/absence of staminate clones (character 36) have high loadings in factor 2. Factor 3 has high loadings for staminate corolla length (character 33) and length of the basal rosette leaves (character 1). *Antennaria aromatica* and *A. densifolia* form two distinct groups (Fig. 3) and disassociate best along factor 1. The diploid and tetraploid cytotypes of *A. aromatica* appear to form two groupings along factor 2. A trend toward the separation of sexual and asexual populations of *A. aromatica*, as expressed by presence/absence of staminate plants, is evident on factor 2. Although two





FIG. 2. Distribution of cytotypes of *Antennaria aromatica* and *A. densifolia* in Montana and Wyoming. Open circles = diploid, closed circles = tetraploid, and star = hexaploid populations of *A. aromatica*. The open square is a diploid population of *A. densifolia*. The continental divide is indicated by the dot/dash line and the Wisconsin glacial maximum, following Prest (1984), is shown by "T" shaped symbols. Bar = 250 km.

subgrouping are apparent within the *A. densifolia* cluster (Fig. 3), it is not certain whether these two represent different ploidy levels.

### DISCUSSION

The direct relationship of *A. aromatica* to *A. densifolia* is indicated by similarity of morphology and ecology. They are part of a larger complex of arctic/alpine *Antennaria* (Alpinae group) and consequently are related to *A. umbrinella* Rydb. and *A. pulchella* E. Greene (Bayer 1987b). Using a taxonomic species concept, *A. aromatica* and *A. densifolia* can be considered discrete species because they are morphologically distinct. The PCA demonstrates this conclusively, and indicates that the presence of stalked glands (and the coincident citronella odor in the living plants) in *A. aromatica* and the complete lack of these glands in *A. densifolia* distinguishes them reliably. Three other characters can be used to separate the two species. Most individuals of *A. densifolia* possess flat, scarious, linear-lanceolate tips, termed "flags", at the ends of the upper cauline leaves (character 18; Table 1), however most *A. aromatica* lack these flags. The basal



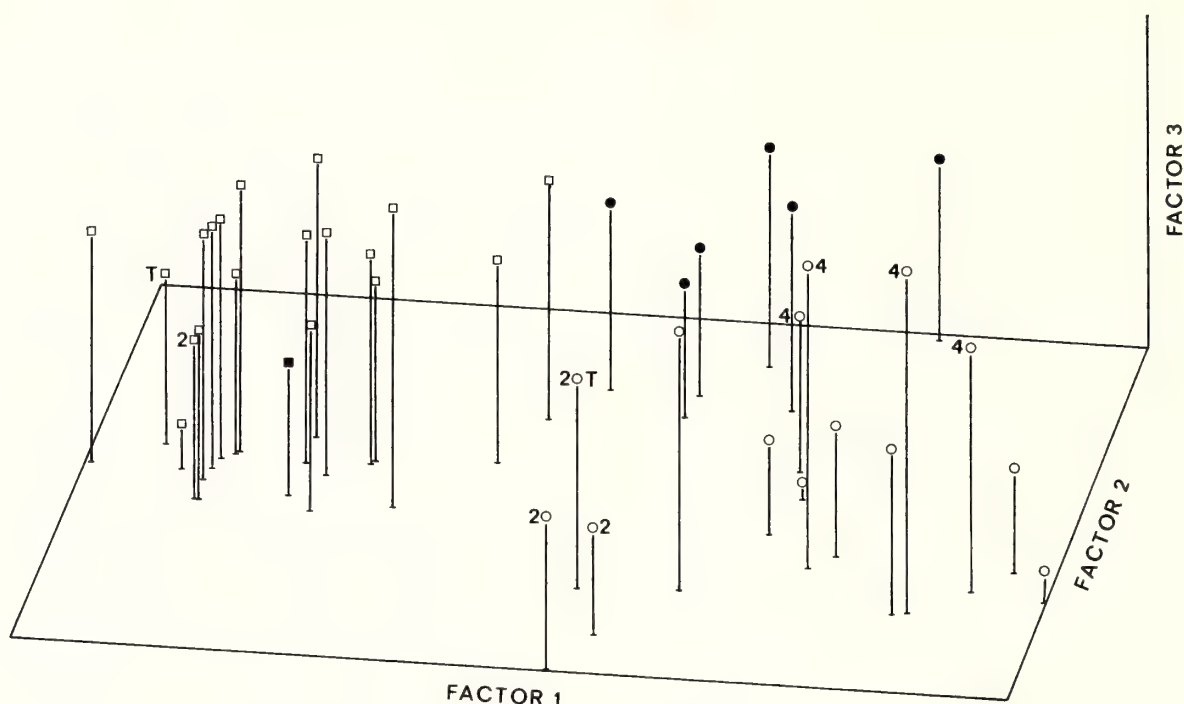


FIG. 3. PCA composed of 20 OTU's of *Antennaria aromatica* (circles) and 20 of *A. densifolia* (squares). Open symbols indicate collections containing pistillate and/or staminate individuals, whereas closed symbols signify collections having only pistillate plants. An isotype of *A. aromatica* (ALTA) and the holotype specimen of *A. densifolia* (CAN) are marked with "T". Specimens of known chromosome number are labeled "2" for diploid and "4" for tetraploid. The one disjunct diploid population of *A. densifolia* from Montana is the open square labeled "2".

rosette leaves (character 1) in *A. aromatica* are 6.0–16.0 mm long (mean  $9.4 \pm 2.9$ ), whereas those of *A. densifolia* are 3.0–6.0(–7.0) mm long (mean  $4.7 \pm 1.1$ ). *Antennaria aromatica* has pistillate phyllaries that are (4.0–)5.0–7.0 mm long (mean  $5.6 \pm 0.76$ ) and those of *A. densifolia* are 3.0–5.0 mm long (mean  $4.1 \pm 0.58$ ). These three characters are not as reliable as presence/absence of glands to separate the taxa, but the character suite is relatively reliable.

*Antennaria aromatica* was first described (Evert 1984) from the Beartooth Mountains of Montana, but has since been collected from several additional sites in Montana, Wyoming, and Alberta. The species is known only from ca. 40 collections (including several duplicate collecting efforts), but is perhaps more common within its rather restricted range than the scant herbarium record would indicate because of the relative inaccessibility of habitats where these plants are known to occur. Several older collections exist in herbaria, but they were not recognized as belonging to a new species. They are most often misidentified as *A. alpina* (L.) Gaertner, *A. media* E. Greene, or *A. umbrinella*.

Since the description of *A. aromatica*, there has been some confusion about its identity and geographic range. In 1898, Greene described *Antennaria pulvinata* from Moose Mountain in the Front



Range of the Rockies west of Calgary, Alberta (Bayer 1989). This taxon is entirely pistillate and resembles *A. aromatica* closely, except it lacks the glandular hairs. These apomicts are polyploids that undoubtedly have *A. aromatica* as one of their sexual progenitors, but probably have other sexual parents as well (Bayer in press a). I have included these apomicts, and others like them, in the *A. rosea* E. Greene polyploid complex, calling them *A. rosea* subsp. *pulvinata* (E. Greene) R. Bayer (Bayer 1989). Recently, Weber (1987) and Hartman and Rottman (1988) reported *A. aromatica* from Colorado, but I would instead identify these plants as *A. rosea* subsp. *pulvinata*.

Authentic *A. aromatica* is a cushion plant that occurs on talus slopes, almost always composed of limestone. The populations occur from just below treeline to alpine, but, in my experience, are often found just at the treeline with the krummholz vegetation. The plants are viscid, and the younger foliage has a strong citronella odor. The populations are usually sexual, having approximately equal proportions of staminate and pistillate clones (Fig. 1). Some of the common associates of *A. aromatica* are *Androsace chamaejasme*, *Anemone multifida*, *Aquilegia jonesii*, *Arctostaphylos uva-ursi*, *Arenaria obtusiloba*, *Astragalus gilviflorus*, *Astragalus kentrophyta*, *Cymopterus hendersonii*, *Draba oligosperma*, *Dryas octopetala*, *Eriogonum androsaceum*, *Eritrichium nanum*, *Haplopappus uniflorus*, *Hedysarum alpinum*, *Hulsea algida*, *Ivesia gordonii*, *Paronychia sessiliflora*, *Pedicularis parryi*, *Phlox caespitosa*, *Phlox hoodii*, *Physaria didymocarpa*, *Potentilla fruticosa*, *Ribes oxycanthoides*, *Valeriana edulis*, and *Zygadenus elegans*.

All populations of *A. aromatica* occur east of the continental divide, predominantly in areas that were unglaciated during the Wisconsinan (Fig. 1). *Antennaria aromatica* could be restricted to the Front Ranges east of the divide as a result of climatic factors, these mountains receiving less rainfall than those to the west in western Montana and eastern Idaho. The main range of the species is from north-central Wyoming, near Cody, north to Glacier National Park, Montana (Fig. 1). Two minimally disjunct populations of *A. aromatica* occur in the Alberta Rockies, which extends the range of the species to the Mountain Park area east of Jasper, Alberta (Fig. 1). These two collections (ALTA #27162 and #32291) are the first of this species from Canada. The collection from Mountain Park is especially significant because this is not only an area with large areas of limestone outcrops, but is an area that has been identified as a glacial refugium (Packer and Vitt 1974; Prest 1984) and is known for its large number of species disjunctions.

*Antennaria aromatica* occurs as both diploid and polyploid races (Table 2). The PCA demonstrates that the two groups (diploids and polyploids) are slightly distinct morphologically (Fig. 3). Although the two cytotypes cannot be reliably distinguished on morphological



grounds, the diploids are mostly smaller in all respects when compared to the polyploids (pistillate involucres in the 3 confirmed diploids are 5.0–6.0 mm high, whereas those of four tetraploids are (6.0–)6.5–7.5 mm high). Similarly to other species of *Antennaria*, populations of the *A. aromatica* diploid cytotypes have equal proportions of staminate and pistillate clones (Bayer unpubl. obs.). Some of the tetraploid populations have both staminate and pistillate plants, whereas others have only pistillate plants (Table 2, Fig. 2). The only known hexaploid population is entirely pistillate (Fig. 2, Table 2). *Antennaria aromatica* conforms to a pattern that appears in several other species of *Antennaria*, such as *A. marginata* and *A. media*, one in which populations of the diploid cytotype within a species are sexually reproducing. Populations of the polyploid cytotype, which are for the most part morphologically indistinguishable from the diploids, are either sexually or asexually reproducing. The diploids frequently have a much more restricted range than the polyploids and are often found strictly in unglaciated regions, whereas the polyploids have wide ranges in both glaciated and unglaciated areas (Bayer and Stebbins 1981). Asexual polyploids are also the ones that usually colonize the areas farthest away from the center of the species range and/or into glaciated terrain. The distribution of cytotypes within *A. aromatica* (Fig. 2) corresponds well to this pattern.

*Antennaria densifolia* was originally described by Porsild (1945) from the east slope of the MacKenzie Mountains, Northwest Territories. Porsild (1945) stated that it superficially resembled *A. pulvinata* E. Greene and *A. compacta* Malte. In Porsild's keys to species for arctic Canada (Porsild 1950; Porsild and Cody 1980), the means of distinguishing *A. compacta* from *A. densifolia* is by the lack of staminate individuals in *A. compacta*, and its longer, more linear, basal leaves.

The habitat of *A. densifolia* is similar to that of *A. aromatica*; i.e., calcareous talus, ranging from subalpine through treeline to alpine. Specimen data suggest that *A. densifolia* occurs most often in alpine situations, and *A. aromatica*, most often in the subalpine or at tree-line.

In constructing the distribution maps of *A. densifolia*, I identified some specimens lacking staminate plants as *A. densifolia* although by using Porsild's key (Porsild 1950) they are *A. compacta*. These specimens have the shorter, cuneate leaves of *A. densifolia* and probably represent the disregard of staminate plants on the collectors' part. Most of these collections were made near other sites where staminates are known to occur (Fig. 1). About 40 populations containing both staminate and pistillate individuals are now confirmed, but many of these sites are very close together along the only roads in the areas, the Dempster highway over the Ogilvie and Richardson mountains and the north Canol road over the MacKenzie Mountains



(unfortunately, the road is now abandoned and impassable in the region where *A. densifolia* is known). The large number of specimens from the southern MacKenzie Mountains in the Nahanni National Park were probably collected during the initial vegetation surveys of this wilderness park. The distribution of *A. densifolia* (Fig. 1) is in two slightly disjunct areas, the eastern slopes of the MacKenzie Mountains, and the northern Ogilvie and southern Richardson mountains. Although *A. densifolia* has not been collected in the remote interlying region, the valley-glaciated Wernecke Mountains, it is possible that it does occur there because dolomitic limestone outcrops exist in this range (Oswald and Senyk 1977). The northern Ogilvies and southern Richardsons had only limited alpine glaciation during the Wisconsinan (Prest 1984). The eastern slope of the MacKenzies were part of the northern end of the western Canadian ice-free corridor (Rutter 1984), but perhaps had restricted alpine glaciers during the Wisconsinan. The majority of the *A. densifolia* populations containing staminate plants are located within the unglaciated regions, only three populations being located in previously glaciated terrain (Fig. 1).

One very noteworthy collection was our (Bayer, DeLuca, and Lebedyk MT-725 at ALTA and RM or Lackschewitz 4611 at MONTU) recent discovery of a population of *A. densifolia* in the Anaconda Range of Granite Co., Montana (Figs. 1 and 2) found growing in gravelly, limestone talus on open alpine tundra. This site represents not only the first collection of the species for the United States, but a substantial (1850 km) disjunction from the nearest population in the Northwest Territories. Morphologically the plants from Montana are well within the range of typical *A. densifolia* from Canada (Fig. 3) and are diploid, the same as the only available count for northern Canadian *A. densifolia* (Table 2).

Although only diploid counts have been obtained for *A. densifolia*, it is probable that some tetraploid populations exist, as two weakly distinct subgroups within *A. densifolia* are present in PCA (Fig. 3). It is possible that this species repeats the pattern of morphologically indistinguishable diploid and sexual polyploid races present within species. Additional chromosome counts are needed to confirm or reject this hypothesis. *Antennaria densifolia* is similar to *A. aromatica*, in that a group of apomicts (*A. compacta*) derived from *A. densifolia* are morphologically very similar to their parent. In a similar manner, there are polyploid apomicts related to *A. aromatica* (*A. rosea* subsp. *pulvinata*). The taxa can be identified by means of the following key.

KEY TO ANTENNARIA AROMATICA, A. COMPACTA, AND A. DENSIFOLIA

- A Basal leaves linear to linear-oblongate, two or more times longer than wide, arising from densely tufted basal caudices. .... *A. compacta*



- A' Basal leaves cuneate to cuneate-spathulate, less than two times longer than wide, densely caespitose and arising from short, prostrate stolons.
- B Stalked glands present on flowering stalks, phyllaries, and leaves; odor of citronella present in living plants; flags usually lacking from upper cauline leaves, basal leaves mostly 6.0 mm or more long; pistillate phyllaries mostly 5.0 mm or more long. . . . . *A. aromatica*
- B' Stalked glands absent from flowering stalks, phyllaries, and leaves; living plants odorless; flags usually present on upper cauline leaves; basal leaves mostly less than 6.0 mm long, pistillate phyllaries mostly less than 5.0 mm long. . . . . *A. densifolia*

The distributions of *A. aromatica* and *A. densifolia* (Fig. 1) provide clues to the phylogeographic and evolutionary history of the two species. It is probable that both species may once have had much wider ranges, and the advance of the Cordilleran and Laurentide ice sheets during the Wisconsinan obliterated the greater part of their former ranges. Sexual dioecism evidently prevents swift migration, as few sexual species of *Antennaria* have extensive ranges in glaciated terrain (Bayer and Stebbins 1987). The solitary population of *A. densifolia* in Montana near the southern end of the ice-free corridor (Fig. 1) may indicate that the species once occurred more widely as far south as Montana and was eliminated from the intervening areas of British Columbia and Alberta. The main body of populations of *A. densifolia* remaining today are in the unglaciated area at the northern end of the corridor (Fig. 1). *Antennaria aromatica* exists at the southern end of the corridor, but the two Alberta populations (Fig. 1) that rest within the corridor itself indicate that the species may have once had a much larger range. The populations near the ice margin and within the ice-free corridor probably survived in situ, because, as pointed out by Packer and Vitt (1974), suitable habitats for other endemic calceophiles exist in the surrounding glaciated region, yet the species that are found within the refugial area in Mountain Park, Alberta have not migrated to them.

*Antennaria aromatica* and *A. densifolia* are obviously very closely related and it is probable that they evolved from the same common ancestor (Bayer in press b). Glaciation was probably the vicariant event that separated the series of populations, and the ensuing isolation perhaps facilitated further divergence.

#### ACKNOWLEDGMENTS

I thank the curators at ALA, CAN, COLO, DAO, ID, MONT, MONTU, and RM for their assistance in obtaining specimens for study. This research was supported by a grant from the Natural Sciences and Engineering Research Council of Canada (NSERC grant #A3797) and a grant from the University of Alberta Central Research Fund (NSERC). I thank Montana botanists Klaus Lackschewitz and Peter Lesica for sending me their additional collections of *A. aromatica*. I also appreciate the duplicate material of *A. aromatica* contributed by Ronald Hartman. I am most grateful to Brett Purdy for his helpful input in this study and for compiling Figures 1 and 2. I thank Meredith Lane, LuDean Marvin, John Packer, Richard Pimentel, Brett Purdy, and



Ledyard Stebbins for providing helpful comments on the manuscript. C. C. Chinnappa is gratefully acknowledged for allowing me to verify the identification of his diploid collection (UAC) of *A. densifolia* from Yukon.

#### LITERATURE CITED

- BAYER, R. J. 1984. Chromosome numbers and taxonomic notes for North American species of *Antennaria* (Asteraceae: Inuleae). *Syst. Bot.* 9:74–83.
- . 1987a. Evolution and phylogenetic relationships of the *Antennaria* (Asteraceae: Inuleae) polyploid agamic complexes. *Biol. Zentralbl.* 106:683–698.
- . 1987b. Morphometric analysis of western North American *Antennaria* Gaertner (Asteraceae: Inuleae). I. Sexual species of sections *Alpinae*, *Dioicae*, and *Plantaginifoliae*. *Canad. J. Bot.* 65:2389–2395.
- . 1989. A taxonomic revision of the *Antennaria rosea* (Asteraceae: Inuleae: Gnaphaliinae) polyploid complex. *Brittonia* 41:53–60.
- . In press a. Investigations into the evolutionary history of the *Antennaria rosea* (Asteraceae: Inuleae) polyploid complex. *Pl. Syst. Evol.*
- . In press b. A phylogenetic reconstruction of *Antennaria* Gaertner (Asteraceae: Inuleae) *Canad. J. Bot.*
- and G. L. STEBBINS. 1981. Chromosome numbers of North American species of *Antennaria* Gaertner (Asteraceae: Inuleae). *Amer. J. Bot.* 68:1342–1349.
- and ———. 1983. Distribution of sexual and apomictic populations of *Antennaria parlinii*. *Evolution* 37:555–561.
- and ———. 1987. Chromosome numbers, patterns of distribution, and apomixis in *Antennaria* (Asteraceae: Inuleae). *Syst. Bot.* 12:305–319.
- CHMIELEWSKI, J. G. and C. C. CHINNAPPA. 1988. Taxonomic notes and chromosome numbers in *Antennaria* Gaertner (Asteraceae: Inuleae) from arctic North America. *Arctic and Alpine Res.* 20:117–124.
- EVERT, E. F. 1984. A new species of *Antennaria* (Asteraceae) from Montana and Wyoming. *Madroño* 31:109–112.
- HARTMAN, E. L. and M. L. ROTTMAN. 1988. The vegetation and alpine vascular flora of the Sawatch Range, Colorado. *Madroño* 35:202–225.
- OSWALD, E. T. and J. P. SENYK. 1977. Ecoregions of Yukon Territory. Canadian Forestry Service, Pacific Forest Research Center, Victoria.
- PACKER, J. G. and D. H. VITT. 1974. Mountain Park: a plant refugium in the Canadian Rocky Mountains. *Canad. J. Bot.* 52:1393–1409.
- PORSILD, A. E. 1945. The alpine flora of the east slope of MacKenzie Mountains, Northwest Territories. *Nat. Mus. Canad. Bull.* 101, Ottawa.
- . 1950. The genus *Antennaria* in northwestern Canada. *Canad. Field-Nat.* 64:1–25.
- and W. J. CODY. 1980. Vascular Plants of the Continental Northwest Territories. *Nat. Mus. Canad.*, Ottawa.
- PREST, V. K. 1984. The late Wisconsinan glacier complex. In R. J. Fulton (ed.), *Quaternary stratigraphy of Canada—a Canadian contribution to IGCP project 24*. Geological Survey of Canada paper 84-10, Ottawa.
- ROHLF, F. J. 1987. NTSYS-pc: numerical taxonomy and multivariate analysis system for the IBM PC microcomputer (and compatibles). Applied Biostatistics, Inc., Setauket.
- RUTTER, N. W. 1984. Pleistocene history of the western Canadian ice-free corridor. In R. J. Fulton (ed.), *Quaternary stratigraphy of Canada—a Canadian contribution to IGCP project 24*. Geological Survey of Canada paper 84-10, Ottawa.
- WEBER, W. A. 1987. Colorado flora: western slope. Colorado Associated Univ. Press, Boulder.

(Received 25 Jan 1989; revision accepted 28 Jun 1989.)



# A RE-EVALUATION OF *BEALIA MEXICANA* (POACEAE: ERAGROSTIDEAE)

PAUL M. PETERSON

Department of Botany, National Museum of Natural History,  
Smithsonian Institution, Washington, DC 20560

## ABSTRACT

Based on morphological and cytological evidence, *Bealia* is recognized as a genus with a single species, *B. mexicana*. This genus may be related to *Dasyochloa* and *Erioneuron* as the three share a base chromosome number of  $x=8$  and a number of morphological features. A key distinguishing *Bealia*, *Dasyochloa*, *Erioneuron*, and *Muhlenbergia* is presented. A full description, illustration, and citation of specimens examined are given for *Bealia mexicana*.

## RESUMEN

En base a la evidencia morfológica y citológica *Bealia* es reconocido como un genero monotípico, conteniendo la especie *B. mexicana*. *Bealia* parece estar relacionado a *Dasyochloa* y *Erioneuron* por el hecho de que los tres géneros comparten el mismo numero básico de cromosomas ( $x=8$ ) y otros tantos caracteres morfológicos. El presente artículo provee una clave para los géneros *Bealia*, *Dasyochloa*, *Erioneuron* y *Muhlenbergia*. Presentase además una descripción comprensiva de *Bealia mexicana*, así como su ilustración y citación de ejemplares estudiados.

During investigations of the annual species of *Muhlenbergia* Schreber (Peterson 1988a, b, 1989a, b; Peterson and Rieseberg 1987; Peterson et al. 1989; Peterson and Annable 1990) it became apparent that a segregate genus should be recognized for *Muhlenbergia biloba*. New information, particularly from chromosome cytology, coupled with numerous unusual morphological characters, supports its placement in *Bealia*. The purpose of this paper is to reinstate *Bealia* as a genus, discuss possible relationships to other eragrostoid genera, and give a complete taxonomic account.

The binomial *Bealia mexicana* was first published, without a description or a diagnosis, by Vasey (1889) and was based on material collected by *Pringle 819* from the mountains of Chihuahua and *Brandege 16* from Santa Margarita Island, Baja California Sur. Charlotte Reeder (1956) later showed that the specimen Brandege collected from Santa Margarita Island represented a new species, *Muhlenbergia brandegei* C. Reeder. I agree with C. Reeder that *M. brandegei* should currently reside in *Muhlenbergia*, however, the placement of the Chihuahuan material is the topic of this paper.

The first valid publication of *Bealia mexicana* was that of Scribner in Beal (1896) who based it on *Pringle 819* from Chihuahua, Mexico.



Jones (1912) transferred the species to *Epicampes*, naming it *E. mexicana*, but Hitchcock (1913) and subsequent workers have treated it as a species of *Muhlenbergia*, *M. biloba*.

The only other combination published in *Bealia*, *B. speciosa* (Vasey) Beal, was based on *Palmer 30* from southwestern Chihuahua. Hitchcock (1913). Soderstrom (1967), and I agree with Vasey in treating it as *Muhlenbergia speciosa* Vasey. Jones (1912) also transferred this species to *Epicampes*, naming it *E. speciosa*. *Epicampes* has been recognized as a section of *Muhlenbergia* subgenus *Podosemum* since Soderstrom's (1967) work.

*Bealia mexicana* has a base chromosome number of  $x=8$  ( $2n=16$ ) and relatively large chromosomes when compared with other species of *Muhlenbergia* (Peterson 1988a). This base number has not been reported for species of *Muhlenbergia* (J. Reeder 1967, 1968; Peterson 1988a). The common base chromosome number in *Muhlenbergia* is based on 10, although *M. filiformis* (Thurb.) Rydb. and *M. vaginata* Swallen possess 9 pairs.

Scribner and Vasey recognized the distinctive morphological features that distinguish *Bealia mexicana* from most other members of *Muhlenbergia*. It has deeply bilobed lemmas with obtuse lobes and pilose to villous glumes that are single-nerved and longer than the lemma. Only *M. argentea* Vasey and *M. lucida* Swallen from southern Chihuahua have deeply bilobed lemmas with obtuse lobes. These two species are currently being investigated as potential members of the genus.

In my investigations of the annual species of *Muhlenbergia*, A UPGMA cluster analysis utilizing 80 morphological and chemical characters depicted *B. mexicana* as a distinct species (Peterson 1988a). The cluster phenogram shows *B. mexicana* with a large phenetic distance of 1.4 and places it near *M. crispiseta* and *M. peruviana*, whose intra-cluster phenetic distance is very small at 0.55 (phenogram distance range is 0.3 to 1.7). These later two species are in the section *Clomena* and superficially resemble *B. mexicana*, but differ in having glabrous, three-nerved and three-toothed second glumes. The glumes of *B. mexicana* are pilose to villous, single-nerved, and entire near the apex.

*Bealia mexicana* shows close affinities with *Dasyochloa* Willd. ex Rydb. (interpreted as a monotypic North American genus) and *Erioneuron* Nash (includes four species in North America) by sharing a base chromosome number of  $x=8$  and relatively large chromosomes (Tateoka 1961; Peterson 1988b). The lemmas of *Dasyochloa*, *Erioneuron*, and *Bealia* are similar. All are three-nerved, emarginate to bilobed, often awned, and pilose with hairs that are associated with either the nerves, margins, and/or lower two-thirds of the lemma. However, *Bealia* differs from *Dasyochloa* and *Erioneuron* in having spikelets with a single floret, soft membranous spikelets,



lemmas with crisped curled to flexuous awns, glabrous rachillas, fusiform caryopses, and an annual habit.

The unusual morphological characters in *B. mexicana* (Fig. 1) of a deeply bilobed lemma with obtuse lobes, pilose to villous glumes that are single-nerved and longer than the lemma, and a chromosome number of  $n=8$ , support the original treatment of *Bealia* as a distinct genus. The following key distinguishes among *Bealia*, *Dasyochloa*, *Erioneuron*, and *Muhlenbergia* using gross morphological features.

- A Spikelets with one floret, rarely two.
  - B Lemmas deeply bilobed, the lobes rounded to obtuse, the lobes 1–1.4 mm long; awn crisped-curved to flexuous, borne between the lobes. . . . . *Bealia*
  - B' Lemmas not deeply bilobed, sometimes minutely bifid, then the teeth usually acuminate to aristate, the teeth less than 1 mm long; awn usually straight to flexuous or awnless. . . . . *Muhlenbergia*
- A' Spikelets with two to many florets.
  - C Panicle short and capitate, usually exceeded by a fascicle of leaves; plants low, creeping, usually stoloniferous. . . . . *Dasyochloa*
  - C' Panicle exserted, open or contracted; plants spreading, erect or decumbent but not stoloniferous. . . . . *Erioneuron*

BEALIA Scribner in Hackel, True Grasses 103. 1890.

BEALIA MEXICANA Scribner in Beal, Grasses N. Amer. 2:267. 1896.—*Bealia mexicana* Scribner in Vasey, nom. nud. Proc. Calif. Acad. Sci. II. 2:212. 1889.—*Bealia mexicana* Scribner in Hackel, nom. nud. True Grasses 103. 1890.—*Epicampes mexicana* (Scribner in Beal) M. E. Jones, Contr. W. Bot. 14:7. 1912.—*Muhlenbergia biloba* A. Hitchc., Contr. U.S. Natl. Herb. 17:294. 1913.—TYPE: MEXICO. Chihuahua: thin soil of dry porphyry mts., near Chihuahua, 7 Oct 1886, *Pringle 819* (lectotype selected herewith, US!; isoelectotypes, MO!, NME!, NY!, UC!, US!, VT!, WIS!).

Slender, tufted annuals (Fig. 1a). Culms much branched at the lower nodes, often caespitose, scabrellous-pubescent, striate, glabrous to minutely pubescent below the nodes, 9–35 cm tall; 0.3–0.5 mm diam. just below the inflorescence, internodes hollow, short, 2–10 mm long. Sheaths keeled, often striate, scaberulous to almost glabrous, longer than the internodes, usually 2–7.5 cm long; margins wide and scarious. Ligules membranous (Fig. 1b), 1.5–3.4 mm long, apex acute or rounded, often irregularly toothed; margins entire, decurrent, usually splitting to form auricles no longer than the ligule (Fig. 1c). Blades flat, involute upon drying, 1–7 cm long, 0.6–1.4 mm wide, scaberulous below and short pubescent above, midnerve and margins whitish-thickened on the abaxial surface. Inflorescence an open panicle (Fig. 1c), 3–10 cm long, 1.5–3.2 cm wide; branches 1 or sometimes 2 per node, 1.8–4.5 cm long, sinuously ascending or flexuous and spreading up to 40° from the culm axis; pedicels





FIG. 1. *Bealia mexicana*, Chihuahua, Mexico (Peterson and Annable 5800). a. Habit. b. Ligule. c. Inflorescence. d. Spikelet. e. Glumes. f. Floret. g. Lemma. h. Palea. i. Stamens, pistil, and lodicules. j. Caryopsis.



slender, scabrous and minutely glandular, 1–5.5 mm long, loosely ascending; nodes per inflorescence 6–16. Spikelets erect to loosely spreading, 1 floret per spikelet (Fig. 1d, f), disarticulating above the glumes. Glumes equal in length (Fig. 1e), grayish-green to almost bicolored with the lower  $\frac{1}{4}$  grayish-green and upper  $\frac{3}{4}$  whitish-green, obtuse, loosely pilose to villous, especially on lower  $\frac{2}{3}$ , faintly 1-nerved, 3.2–4.8 mm long, as long or longer than the lemma. Lemmas 3-nerved, 2.9–3.5 mm long loosely to densely appressed-villous on the lower  $\frac{2}{3}$  (Fig. 1g), hairs tawny, up to 0.7 mm long; lateral nerves evident on lower half; apex deeply bilobed, 1–1.4 mm deep, lobes rounded to obtuse; awn born between the 2 lobes, scabrous and crisped-curved to flexuous, 4–6.5 mm long. Paleas 2-nerved (Fig. 1h), 2.6–3.4 mm long, about as long as lemma, apex obtuse, loosely to densely appressed-villous on the lower  $\frac{2}{3}$ , hairs like those on the lemma. Stamens 3 (Fig. 1i), anthers 1.2–2.3 mm long, purplish. Caryopsis (Fig. 1j) ca 1.8 mm long, fusiform, olive-brown. Chromosome number,  $n=8$ .

*Habitat, distribution, and phenology.* Shallow, sandy, whitish soils derived from calcareous parent material on flat escarpments associated with rock outcrops in pinyon-juniper woodlands and yellow pine forests, 2000–2300 m elevation. Central Chihuahua to northern Durango, Mexico, known from very few localities. Flowering from Sep through Oct.

*Specimens cited.* MEXICO. Chihuahua: Majalca, 16 Sep 1935, *LeSueur Mex-026* (GH, MO, UC); 15 mi E of El Vergel on road to Parral, 21 Oct 1959, *Correll and Gentry 23270* (GH, MO, UC); Sierra Madre Occidental, 1.2 mi W of Cumbres de Majalca, 22.6 mi W of Hwy 45, Campamento in Parque Nacional, 20 Sep 1986, *Peterson and Annable 4529* (ARIZ, ENCB, GH, MEXU, MICH, MO, NMC, NY, RSA, TAES, UC, US, UTC, WIS, WS), 22 Sep 1988, *Peterson and Annable 5800* (US); 12 mi S of Villa Matamoros, 27 Sep 1988, *Peterson and Annable 5976* (US). Durango: Barranca below Sandia Station, 12 Oct 1905, *Pringle 10147* (GH, UC, MO); Sierra Madre Occidental, ca. 6 mi SW of El Ojito and 40 mi SW of Parral on Hwy 24, 24 Sep 1986, *Peterson and Annable 4570* (ARIZ, ENCB, GH, MEXU, MICH, MO, NMC, NY, RSA, TAES, UC, UNLV, US, UTC, WIS, WS).

#### ACKNOWLEDGMENTS

This study was supported by grants from the National Science Foundation to Amy Jean Gilmartin and PMP (BSR-861211), Sigma Xi, WSU, and the Smithsonian Institution. Special thanks are given to Carol R. Annable for assistance in the field and Alice Tangerini for providing the illustration. I am grateful to Carol R. Annable, Mary E. Barkworth, Amy Jean Gilmartin, Stephen L. Hatch, and David J. Keil for critically reading the manuscript and Pedro Acevedo for preparing the Spanish abstract.



## LITERATURE CITED

- BEAL, W. J. 1896. Grasses of North America, Vol. 2. Henry Holt, New York.
- HITCHCOCK, A. S. 1913. Mexican grasses in the United States National Herbarium. Contr. U.S. Natl. Herb. 17:181–389.
- JONES, M. E. 1912. New species and notes. Grass notes. Contr. W. Bot. 14:1–21.
- PETERSON, P. M. 1988a. Systematics of the annual *Muhlenbergia* (Poaceae). Ph.D. dissertation. Washington State Univ., Pullman.
- . 1988b. Chromosome numbers in the annual *Muhlenbergia* (Poaceae). Madroño 35:320–324.
- . 1989a. Lemma micromorphology in the annual *Muhlenbergia* (Poaceae). Southw. Naturalist 34:61–71.
- . 1989b. *Muhlenbergia majalcensis* (Poaceae: Eragrostideae), a new species from Chihuahua, Mexico. Syst. Bot. 14:316–319.
- and C. R. ANNABLE. 1990. Systematics of the annual *Muhlenbergia* (Poaceae: Eragrostideae). Syst. Bot. Monographs (in press).
- , ———, and V. R. FRANCESCHI. 1989. Comparative leaf anatomy in the annual *Muhlenbergia* (Poaceae). Nordic J. Bot. 8:575–583.
- and L. H. RIESEBERG. 1987. Flavonoids of the annual *Muhlenbergia*. Biochem. Syst. Ecol. 15:647–652.
- REEDER, C. G. 1956. *Muhlenbergia brandegei*, a new species from Baja California, Mexico and its relationship to *Muhlenbergia biloba*. Madroño 13:244–252.
- REEDER, J. R. 1967. Notes on Mexican grasses VI. Miscellaneous chromosome numbers. Bull. Torrey Bot. Club 94:1–17.
- . 1969. Notes on Mexican grasses VIII. Miscellaneous chromosome numbers. Bull. Torrey Bot. Club 95:69–86.
- SODERSTROM, T. R. 1967. Taxonomic study of subgenus *Podosemum* and section *Epicampes* of *Muhlenbergia* (Gramineae). Contr. U.S. Natl. Herb. 34:75–189.
- TATEOKA, T. 1961. A biosystematic study of *Tridens* (Gramineae). Amer. J. Bot. 48:565–573.
- VASEY, G. 1889. Gramineae. Pp. 210–214 in T. S. Brandege, A collection of plants from Baja California. Proc. Calif. Acad. Sci. II. 2:117–216.

(Received 30 Jan 1989; revision accepted 3 Jul 1989.)

## ANNOUNCEMENT

## NEW PUBLICATION

FRYXEL, P. A., Malvaceae of Mexico, *Systematic Botany Monographs*, Vol. 25, pp. [i–ii], 1–522, color fp. 13 Dec 1988, ISSN 0737-8211, ISBN 0-912861-25-8 (hardbound), \$40.00 U.S., \$42.00 foreign, post-paid (from Systematic Botany Monographs, University of Michigan Herbarium, Ann Arbor, MI 48109-1057, with checks payable to “ASPT”). [A monumental opus, on 55 gen. (incl. *Allosidastrum*, gen. nov.), 372 spp. (184 endemic), 10 infraspecific taxa, with introductory sections on endemism, diversity, familial subdivisions, specialized characters, common names, the massive taxonomic part (448 pp.), and concluding biblio., appendices (chief references on important collectors of Mexican plants; new sections in *Hibiscus*, by O. J. Blanchard), species list, and indices to specimens and scientific names.]



A NEW SPECIES OF *DAPHNOPSIS* (THYMELAEACEAE)  
FROM BAJA CALIFORNIA SUR, MEXICO

DENNIS E. BREEDLOVE

Department of Botany, California Academy of Sciences,  
San Francisco, CA 94118

JOSÉ LUIS LEÓN DE LA LUZ

Centro de Investigaciones Biologicas de Baja California Sur,  
La Paz, Baja California Sur, Mexico 23000

ABSTRACT

***Daphnopsis lagunae***, a new species from the highest ridges of the Sierra de la Laguna, Baja California Sur, Mexico, is described. This is a locally restricted species which is the first record for the genus and the family (Thymelaeaceae) for the peninsula of Baja California.

RESUMEN

Se describe una nueva especie de los picachos de la Sierra de la Laguna, Baja California Sur, Mexico: ***Daphnopsis lagunae***. Se trata de una especie con habitat sumamente restringido, es tambien la unica representante del genero y de la familia (Thymelaeaceae) para la peninsula de Baja California.

Fruiting specimens of this *Daphnopsis* were first collected by M. E. Jones in 1930. Subsequently, Breedlove and Axelrod in 1977 and León de la Luz in 1985 made several additional fruiting collections. Although the plant was obviously related to *Daphnopsis* no attempt could be made to further identify it without flowers. León de la Luz, in the course of his studies on the vegetation of the Sierra de la Laguna (León de la Luz and Domínguez 1989), returned to the region three times in spring and summer and finally collected flowering plants in mid-August of 1987 immediately following the first summer rains. It is a curious aside that T. S. Brandegee, who made exhaustive collections in the Sierra de la Laguna at the end of the last century, never encountered this distinctive shrub. A search of the herbarium at the University of California, where the major set of T. S. Brandegee's collections are deposited, was made to no avail. The short period of anthesis which occurs for 6 to 10 days following the inception of the erratic summer rains and the very local nature of this plants distribution best accounts for its absence from his collection. *Daphnopsis lagunae* is the only member of the Thymelaeaceae known from Baja California (Wiggins 1980). *Daphnopsis* is the largest genus, with about 50 species, in the family in the New



World and has three areas with concentrations of species, Mexico, the Antilles and Brazil (Nevling, 1959).

***Daphnopsis lagunae*** Breedlove & León de la Luz, sp. nov. (Fig. 1).—

TYPE: MEXICO. Baja California Sur: Municipio of La Paz, Sierra de la Laguna, Pine Oak forest along trail from La Laguna to El Picacho, 1900 m, 23°31'N, 110°02'W, 14 Aug 1987 (female plant), *León de la Luz* 2730 (holotype Cas; isotypes CIB, UC, MEXU).

Frutex deciduus usque ad 1.5 m altus. Folia coriacea, 4–8 cm longa, 2–5 cm lata, margine revoluta. Inflorescentiae pistillatae et stamineae portatae in pedunculi 1–5 mm longa cum 1–5 floribus. Flores staminales cum calycis tubus anguste obconicus, 6.5–7 mm longa, 1–1.5 mm lata basi, 3.5–4 mm lata orificii, extra tomentosus, intus glaber, petala 8, circa 0.3 mm longa, staminibus in planus 2, disco annulari. Flores pistillates cum calycis tubus 5–6 mm longa, 1.5–2 mm lata basi, 2–2.5 mm lata orificii.

Deciduous, sparsely branched, dioecious shrubs to 1.5 m tall, young branches appressed tomentose. Leaves alternate, estipulate, sessile, coriaceous, 4–8 cm long, 2–5 cm wide, elliptic to lanceolate, glabrous to appressed tomentulose; apex acute to rounded; base cuneate to rounded; margins entire and revolute; venation pinnate with 8–10 ascending primary veins, secondary veins prominently reticulate and partially obscuring the primary veins, midvein prominent beneath, all veins reddish brown on the under surface, immersed and lightly differentiated on the upper surface. Inflorescence an umbel borne from leafy stems of recent growth, rachis appressed pubescent. Staminate inflorescence with the peduncle 8–12 mm long; staminate flowers 2–3(–5) per inflorescence; pedicel 0.5–1 mm long; calyx tube narrowly obconic, 6.5–7 mm long, 1–1.5 mm broad at base, 3.5–4 mm broad at orifice, appressed tomentose outside, glabrous within; calyx lobes unequal, puberulent within, the outer lobes 2 mm long, 1.5 mm broad at base, the inner lobes 2 mm long, 1 mm broad at base, all acute; petals 8, papilliform, about 0.3 mm long, inserted above and to each side of the 4 alternisepalous stamens; stamens 8, inserted at 2 levels; antisepalous stamens inserted at the level of the orifice, exserted; alternisepalous stamens inserted 1 mm below the orifice, included; filaments 0.2 mm long; anthers oblong-ovate, 0.7–1 mm long, 0.3–0.5 mm broad; disc annular, irregularly adnate to the calyx tube base, undulate to irregularly lobed, glabrous, free marginally; pistillode ten pin shaped, 0.7–1.5 mm long, glabrous. Pistillate inflorescences with the peduncles 5–12 mm long; pistillate flowers 1–4 per inflorescence; pedicels 4–6 mm long; calyx tube obconic to narrowly campanulate, 5–6 mm long, 1.5–2 mm broad at the base, 2–2.5 mm broad at orifice, ap-



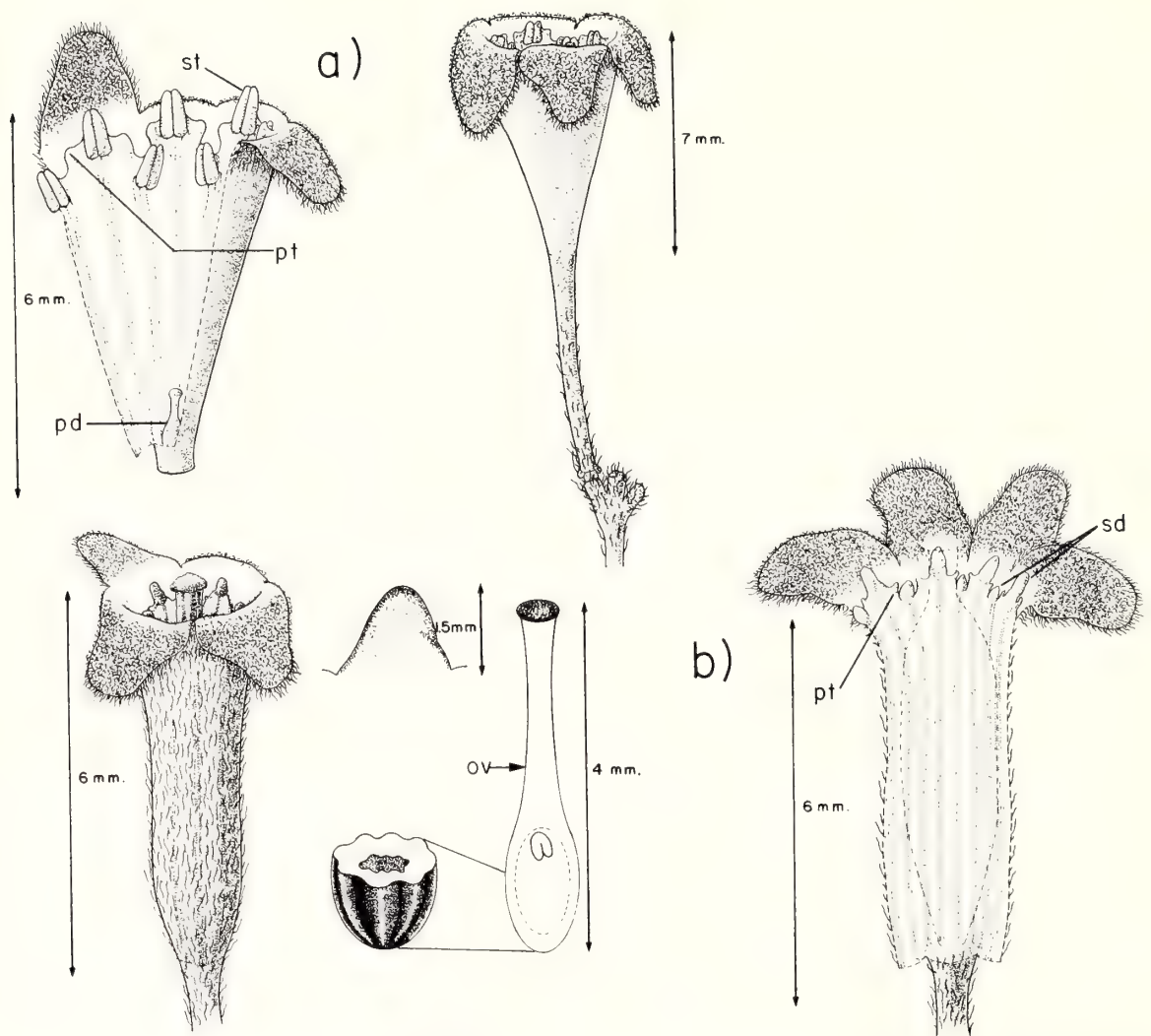
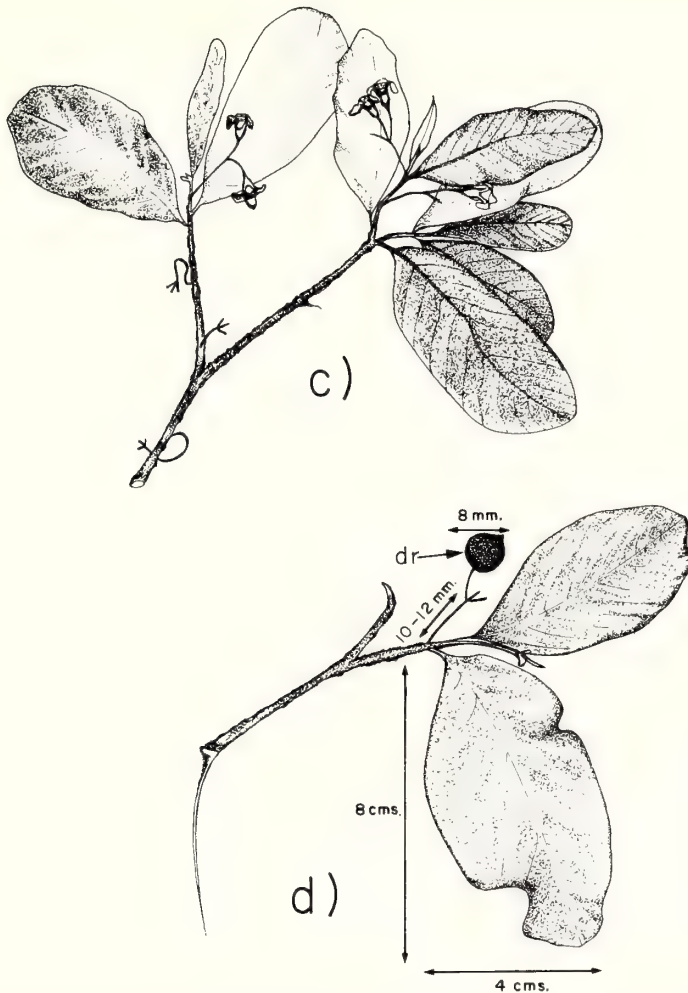


FIG. 1. *Daphnopsis lagunae* Breedlove & León de la Luz a, Staminate flower: (pd) pistillode, (pt) petal, (st) stamen. b, Pistillate flower: (ov) ovary, (pt) petal, (sd) stam-

pressed tomentose outside, glabrous within; calyx lobes subequal, 1–1.5 mm long, 1–1.5 mm broad at the base, puberulent within, apex acute; petals 8, papilliform; staminodia 8, papilliform, difficult to distinguish from the petals; pistil 5.5–6.5 mm long, the stigma capitate, exserted. Drupe ovoid, 8–11 mm long, apiculate, 1–4 maturing per inflorescence, calyx persistent. Seed smooth, brown, spherical, 4–6 mm across; hilum a small depressed black dot on the proximal end.

*Paratypes* MEXICO, Baja California Sur, type locality: 30 Oct 1985, Domínguez 37 (CAS, CIB) fruit; 12 Aug 1987, León de la Luz 2678 (CAS, CIB) male; León de la Luz 2679 (CAS, CIB) female; 14 Aug 1987, León de la Luz 2731 (CAS, CIB) female. Trail from La Burrera to La Laguna: 24 Sep 1930, M. E. Jones 27276 (CAS) fruit; 22 Oct 1977, Breedlove and Axelrod 43308 (CAS) fruit, Breedlove and Axelrod 43376 (CAS) fruit, 14 Aug 1987, León de la Luz 2677 (CAS, CIB) male; León de la Luz 2732 (CAS, CIB) male; 28 Aug 1987, León de la Luz 2817 (CAS, CIB) female. Cerro Verde: 12 Sep 1986, León de la Luz 2032 (CAS, CIB) fruit.





inode. c, branch in flower. d, branch in fruit. Floral tube drawings by Colleen Sudekum, habit and ovary drawn by J. L. León de la Luz.

*Distribution.* Known from three populations in the Sierra de la Laguna. The largest population occurs near the summit of El Picacho (2000 to 2150 m) and extends south as scattered individuals along the ridge facing the Pacific Ocean to at least the point where the trail from La Burrera crosses to La Laguna where a second large population exists. A small population with only a few plants has been found near the summit of El Cerro Verde.

*Habitat.* All of the populations occur on unstable, rocky, granitic soils in both shaded and exposed situations on steep slopes or on relatively flat ridge tops. The associated species include: *Arbutus peninsularis* Rose & Goldman, *Arracacia brandegei* Britton & Rose, *Bernardia lagunensis* (M. E. Jones) Wheeler, *Calliandra peninsularis* Rose, *Cyclanthera tamnoides* Cogn., *Helianthus similis* (Brandeggee) S. F. Blake, *Lepechinia hastata* (A. Gray) Epling, *Mimosa xantii* A. Gray, *Mirabilis jalapa* L., *Nolina beldingii* Brandeggee, *Pinus lagunae* (Passini & Bailey) Passini, *Quercus devia* Goldman, *Quercus tuberculata* Liebm., *Tagetes lacera* Brandeggee, *Tephrosia canna* Brandeggee, *Verbesina pustulata* M. E. Jones, and others.



## DISCUSSION

Nevling (1959) in his excellent revision of the genus *Daphnopsis* does not delimit species groups as such and states that species that have the same level of development of petal type may or may not be related. *Daphnopsis lagunae* with eight petals and a few-flowered inflorescence seems morphologically distant from the species that is closest geographically, *D. mexiae* Nevling of Nayarit and Sinaloa, which has the petals connate into a faucal annulus and an umbellate inflorescence with up to 55 flowers. Of the seven species with eight petals, one from the Antilles, three from northern South America and three from Mexico, most are from wet forest locations and none share three or more of the key characters used by Nevling. *Daphnopsis lagunae* appears to be unique within the genus. Its markedly deciduous habit, few-flowered inflorescence and eight petals clearly set it apart from other species.

## ACKNOWLEDGMENTS

The authors wish to express special thanks to Annetta Carter for her encouragement and advice in the preparation of this manuscript. Dr. Arturo Gomez-Pompa, Director of the UC MEXUS Program, provided support for León de la Luz to visit the herbaria of the University of California and the California Academy of Sciences to begin this study. This research has been partially funded by a grant from CONACYT-SPP, Mexico.

## LITERATURE CITED

- LEÓN DE LA LUZ, J. L. and R. DOMÍNGUEZ 1989. Flora of the Sierra de la Laguna, Baja California Sur, Mexico. *Madroño* 36:61–83.  
NEVLING, L. I., JR. 1959. A revision of the genus *Daphnopsis*. *Ann. Missouri Bot. Gard.* 46:257–358.  
WIGGINS, I. L. 1980. Flora of Baja California. Stanford Univ. Press. 1025 pp.

(Received 9 May 1989; revision accepted 28 Aug 1989.)

## ANNOUNCEMENT

## NEW PUBLICATION

GOODRICH, S. and E. NEESE, *Uinta Basin flora*, USDA Forest Service—Intermountain Region, Ogden, UT, 1986, [iii], xvii, 320 pp., 1 foldout map, unillus., no ISBN, paperbound, price unknown. [Reproduced from single-spaced camera-ready copy. On ca. 1660 specific and sub-specific taxa from a ca. 40,000 km<sup>2</sup> area in Utah and Colorado. For review see J. Major, *Fremontia* 15(4):30.]



**MONARDELLA BENEOLENS (LAMIACEAE), A NEW  
SPECIES FROM THE CREST OF THE SOUTHERN  
SIERRA NEVADA, CALIFORNIA**

**JAMES R. SHEVOCK**

Department of Botany, California Academy of Sciences,  
San Francisco, CA 94118-4599

**BARBARA ERTTER**

University and Jepson Herbarium, University of California,  
Berkeley, CA 94720

**JAMES D. JOKERST**

Department of Botany, California Academy of Sciences,  
San Francisco, CA 94118-4599

**ABSTRACT**

***Monardella beneolens***, a new species from the crest of the southern Sierra Nevada in Inyo, Kern, and Tulare counties, California, is described and illustrated. The new species is ecologically and morphologically closest to *M. cinerea* of subalpine and alpine habitats in the San Gabriel Mountains, Los Angeles and San Bernardino counties, southern California. The sessile, ovate, undulate-crisped leaves; abundant short-stalked glandular hairs on the leaves, bracts, and calyces; and longer spreading eglandular hairs throughout collectively distinguish *M. beneolens* from all other species of *Monardella*.

The existence of this distinctive, sweet-smelling *Monardella* first came to the authors' attention in June 1986 during a botanical collecting expedition to Owens Peak. A subsequent search of *Monardella* collections at CAS, DS, JEPS, RSA, UC, and UCSB revealed five collections of comparable material, labelled as *M. odoratissima* Benth. subsp. *parvifolia* (E. Greene) Epling. Among these was an undetermined vegetative specimen collected by C. A. Purpus in July 1896 on Olancha Peak that represents the first collection of this new species. It was later collected at Olancha Peak in 1950 by J. T. Howell and in 1975 by James Tatum, who was doing a flora of the peak for his master's thesis (Tatum 1979). Clare Hardham, a student of *Monardella* and author of several endemic California species in this genus, annotated Howell's collections as an "undescribed species" in 1975. She was never able to study mature material and consequently did not formally describe the species.

***Monardella beneolens*** Shevock, Ertter, & Jokerst, sp. nov. (Fig. 1).—

TYPE: USA, California, Kern Co., near the summit of Owens



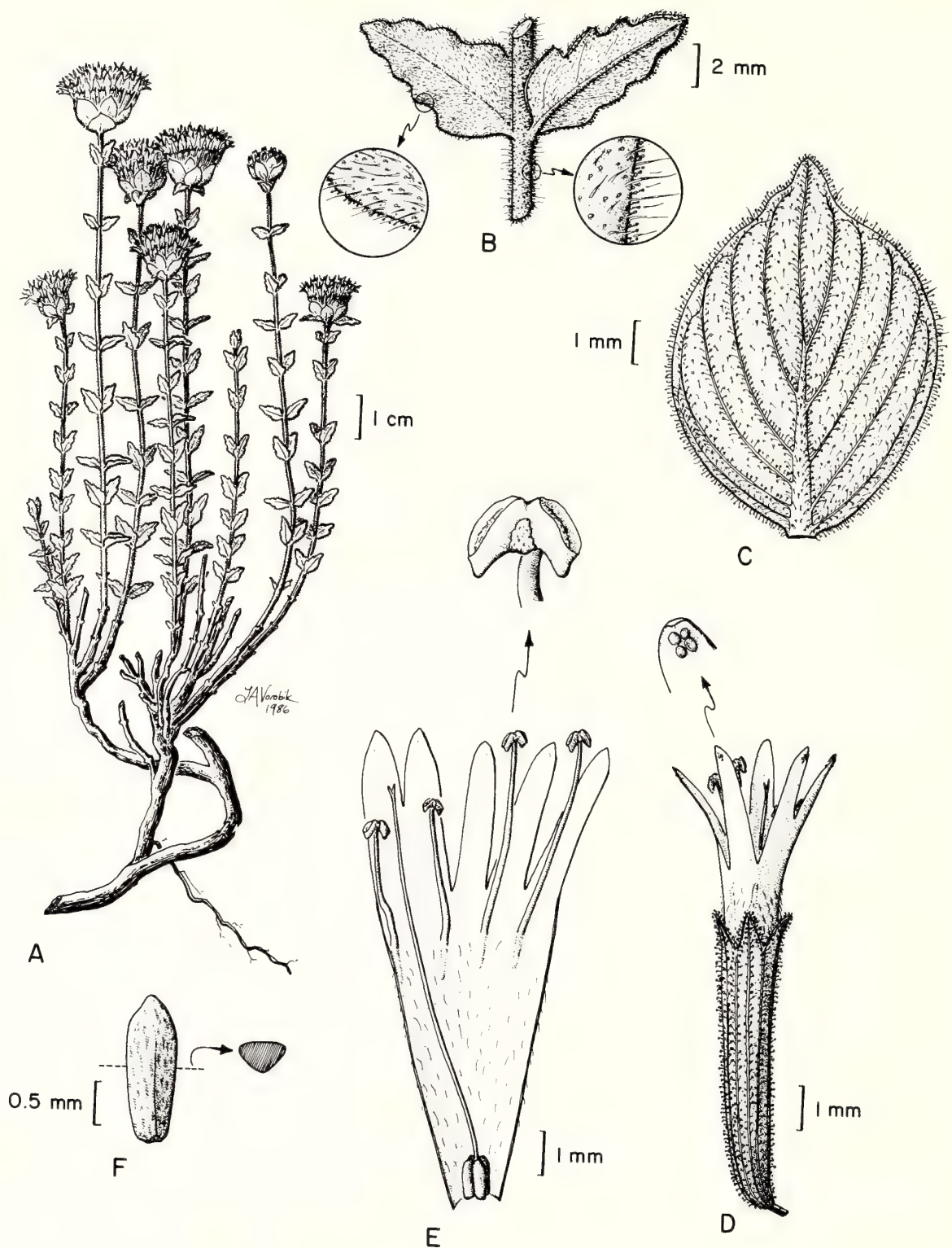


FIG. 1. *Monardella beneolens*.—A, habit; B, leaves with close-up of vestiture; C, outer leafy verticillaster bract; D, flower with glandular droplets at corolla tip; E, internal structure of corolla with enlargement of anther; F, nutlet with cross-section.

Peak on granitic and metamorphic scree and bedrock, open mixed conifer forest, eastern slope below the Sierran crest, T26S R37E sect. 21, 8200 ft. (2500 m), 13 Jul 1986, *Shevock, Bartel, and York 11727* (holotype: CAS; isotypes: FSC, MO, NY, RSA, UC).



Ab aliis *Monardella* combinatione habitu laxe rhizomatosa, glandulis abundis stipitatus trichomatibus villosis, foliis ovatis sessilibus crenatis undulatis distinguenda.

Mat-forming, loosely rhizomatous perennial, vestiture a mixture of abundant fine glandular hairs  $\pm 0.1$  mm long and spreading non-glandular hairs  $\pm 1$  mm long. Stems erect, 0.7–3 dm high, sometimes branched above, villous, bark light brown below and green above. Leaves 5–13 pairs per stem, short petiolate to nearly sessile, those near the ground largest; blades ovate, densely hairy on both surfaces, margin undulate,  $\pm$  crenate, 7–15 mm long and 2–10 mm wide. Verticillaster (head), solitary or occasionally with 1–2 additional heads in distinct whorls below, or in a panicle. Verticillaster bracts in three sets: outer set 2 pairs, 6–9 mm long, 4–7 mm wide, ovate, acute, scarious or the outer pair leaflike or leafy-tipped with green, undulate margins, scarious portions occasionally rose or lavender, closely subtending head or the outer pair 1–5(–8) mm distant; middle set of bracts 2–3 pairs, lance-ovate, scarious, rose to lavender aging to straw-colored; inner set of bracts 0–3(–5), lanceolate or acicular, scarious. Calyx 6–8 mm long, sparsely to moderately hairy with short and long glandular hairs, 13–15 veined; lobes triangular-acute, margins glandular-ciliate with hairs to 0.5 mm long. Corolla 9–11 mm long, tube exerted from calyx  $\frac{1}{6}$  to  $\frac{1}{8}$  its total length, lavender to pale rose, sparsely pilose within and more densely so without; lobes tipped with gold colored glandular droplets, upper lip cleft  $\frac{1}{2}$  its length; stamens unequal, with lower pair equal to or exceeding the corolla lobes and upper pair shorter than corolla lobes, filaments attached near or below the middle of the corolla; pistils shorter than the stamens, stigma branches  $< 1$  mm long; nutlets 1.5–2.0 mm long, triangular-ovate in cross section, light brown with black mottling. Chromosome number  $n=21$ .

*Paratypes*: USA, California, Kern Co., type locality, 2500 m, 11 Jun 1986, *Ertter, Daniel, and Bagley 6443* (UC); 8 Sep 1987, *Shevock and Jokerst 11812* (CAS, RSA, UC). Tulare Co., Olancho Peak, W slope of summit at base of granitic boulders above foxtail pine forest, T19S R36E sect. 19 NE $\frac{1}{4}$  SW $\frac{1}{4}$ , 11,600 ft (3530 m), 22 Jul 1950, *Howell 27202* (CAS); Olancho Peak, Jul 1896, *Purpus 1866* (UC). Inyo Co., Olancho Peak, southern saddle at timberline, T19S R36E sect. 19, 10 Sep 1986, 10,700 ft (3260 m), *Shevock 11771* (CAS, FSC, MO, NY, RSA, UC); SE shoulder of Olancho Peak, 3402 m, 29 Jul 1975, *Tatum 220* (UCSB); S ridge of Olancho Peak, 3353 m, no date, *Tatum 502* (UCSB); Little Cottonwood Creek, 10,200 ft (3110 m), 12 Aug 1949, *Howell 26254* (CAS).

*Distribution, habitat and phenology.* *Monardella beneolens* grows on rocky granitic or metamorphic slopes in open mixed conifer and foxtail pine forests, from 2500 to 3530 m. Plants form extensive



dense mats 1.5 m or more across where rooting substrate consists of rocky scree. Plants in bedrock crevices and ledges are smaller. Flowering extends from July to September, depending on elevation, snowpack duration, and patterns of seasonal aridity.

*Monardella beneolens* is known from only three sites along the southern Sierra Nevada crest: Owens Peak in Kern County, Olancho Peak in Inyo/Tulare counties, and Cottonwood Creek in Inyo County (Fig. 2). Although *M. beneolens* is not associated with a consistent group of species at these three populations, it occurs with a surprisingly high concentration of rare localized southern Sierra Nevada endemics. Noteworthy associates include *Eriogonum wrightii* Torrey ex Benth. var. *olanchense* (J. T. Howell) Rev. and *Trifolium dedekerae* G. Gillett at Olancho Peak; while *Erigeron aequifolius* H. M. Hall, *Eriogonum breedlovei* (J. T. Howell) Rev. var. *shevockii* J. T. Howell, *Haplopappus gilmanii* S. F. Blake, *Lomatium shevockii* R. L. Hartman & Constance, and *Raillardella muirii* A. Gray occur at Owens Peak.

*Morphological variation and hybridization.* Populations of *Monardella beneolens* from Olancho and Owens Peak are quite distinct. Olancho Peak material from above timberline, has generally shorter stems, denser villous and glandular hairs, and smaller crisped leaves. This may be a function of climate since Olancho Peak populations occur nearly 770 meters higher in elevation than those on Owens Peak.

Below timberline south of Olancho Peak, possible hybridization with *M. linoides* A. Gray has been observed. The apparent hybrids are taller than *M. beneolens*, with narrower, less crisped leaves, and bracts exceeding the calyces with parallel veins that branch from the midrib near its base. In addition, plants from *Shevock 11762* (along the Pacific Crest Trail S of Olancho Peak) with petiolate leaves, fascicles of undeveloped leaves in the axils, longer internodes, and softly pubescent calyces may be hybrids between *M. beneolens* and *M. odoratissima*, a relative of *M. linoides*. Given the propensity for hybridization in *Monardella*, ecological rather than genetic factors appear to be most responsible for maintaining what distinctions exist among sympatric species (Epling 1925; Hardham 1966; Hardham and Bartel in press).

Owens Peak was selected for the type locality because plants there display the least hybridization of the *M. beneolens* populations known. This contrasts with Clare Hardham's (pers. comm.) belief that the Olancho Peak material is the least hybridized and therefore more suitable as the type.

In our understanding, plants from Owens Peak have traits that could be interpreted as ancestral to the Olancho Peak population while the converse seems less tenable. In addition to exhibiting the



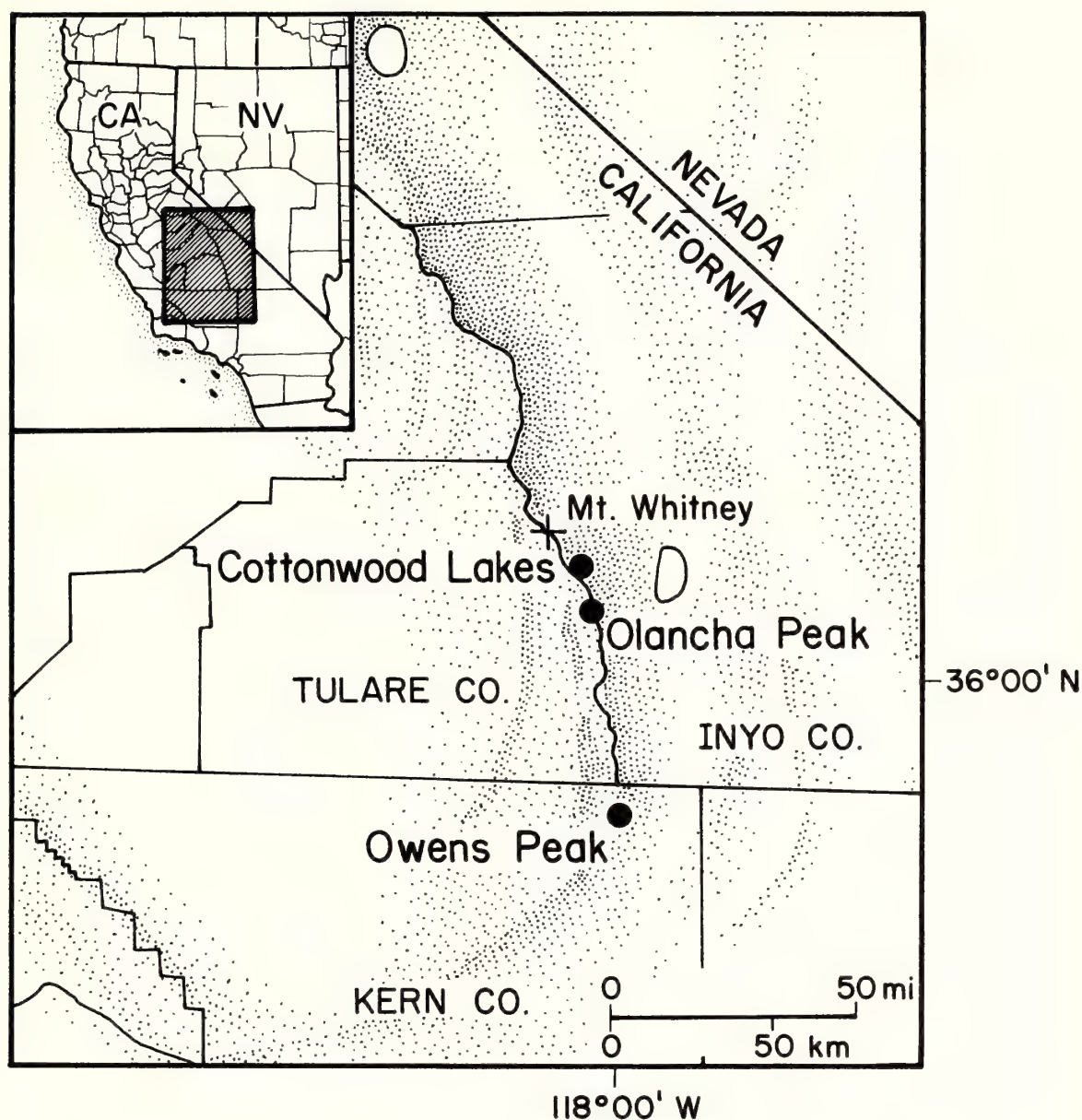


FIG. 2. Distribution of *Monardella beneolens* along the crest of the southern Sierra Nevada in Inyo, Kern, and Tulare counties, California.

fewest traits of other locally occurring species, plants from Owens Peak more closely resemble other geographically restricted *Monardella* from southern California and Arizona. It is likely that *M. beneolens* was historically more widespread and the isolated populations we observe today have since diverged as a result of hybridization and other forces.

*Relationships.* Unlike many species of *Monardella*, which are often not well delimited, *M. beneolens* is so distinct in its combination of openly rhizomatous habit, ovate crenate-undulate leaves, and mixed short glandular and spreading villous vestiture, that determining its relationships is challenging. The existence of putative hybrids with sympatric *Monardella* could lead one to conclude that *M. beneolens* is closely related to *M. linoides* and *M. odoratissima*. These latter



TABLE 1. CHARACTERS USED TO DIFFERENTIATE *MONARDELLA BENEOLENS* AND OTHER CLOSELY RELATED SPECIES.

|                      | <i>M. BENEOLENS</i>   | <i>M. CINEREA</i>  | <i>M. ARIZONICA</i>  |
|----------------------|---|--|--|
| Leaves               |   |  |  |
| Attachment           | sessile   | sessile to short-petiolate   | sessile to minutely petiolate  |
| Blade shape          | triangular-ovate  | ovate to triangular-ovate  | linear to oblong-lanceolate  |
| Base shape           | rounded-obtuse to $\pm$ cordate   | rounded-obtuse to $\pm$ cordate  | rounded-acute  |
| Apex shape           | sharp acute   | sharp acute  | rounded-acute  |
| Margin               | $\pm$ toothed, undulate   | $\pm$ toothed, faint undulate in some  | entire and plane   |
| Vestiture types      | 1) moderately dense, non-glandular hairs<br>2) moderately dense, glandular hairs with tip $2 \times$ width of stalk<br>3) stalked, gold-colored, glandular droplets | 1) dense, non-glandular hairs<br>2) dense glandular hairs with tip $< 1.5 \times$ width of stalk<br>3) sessile, gold-colored, glandular droplets matted on underside | 1) dense, non-glandular hairs<br>2) dense glandular hairs with tip $2 \times$ width of stalk, these concealing the lower leaf surface<br>3) stalked, gold-colored glandular droplets |
| Bract                |   |  |  |
| Habit                | involucrate and overlapping thus concealing calyx bases; outer spreading in some  | weakly involucrate or not overlapping, only partially concealing calyx bases; outer reflexed in some   | narrow, not involucrate or concealing calyx base; outer reflexed   |
| Shape                | ovate, acute  | ovate, acute   | broadly lanceolate, acute  |
| Venation             | parallel pinnate  | parallel pinnate to dendritic  | parallel pinnate   |
| Texture              | outer leaflike in some, remainder scarios   | outer scarios to leaflike, remainder scarios   | outer leaflike, remainder scarios  |
| Color at anthesis    | straw to rose   | purple to red  | green to straw   |
| Color after anthesis | straw   | purple to red  | straw  |



TABLE 1. CONTINUED.

|                          | <i>M. BENEOLENS</i>   | <i>M. CINEREA</i>   | <i>M. ARIZONICA</i>  |
|--------------------------|---|---|--|
| Corolla                  |   |   |  |
| Tube exertion from calyx | 1/8 to 1/8 the length of corolla tube   | tube not exerted  | ± 1/4 the length of corolla tube   |
| Gland at apex            | yes   | no  | yes  |
| Color                    | lavender to pale rose   | pale lavender   | white to occasionally rose tinged  |
| Calyx                    |   |   |  |
| Vestiture                | dense amounts of long & short glandular hairs   | scant amounts of hairs  | scant to moderate amounts of glandular and eglandular hairs              |
| Lobes shape              | triangular acute  | long acuminate  | long acute   |
| Lobes margin             | glandular ciliate from hairs originating on raised "berm" of tissue on outer edge of lobes  | glandular ciliate from hairs originating on raised "berm" of tissue on outer edge of lobes          | appearing ciliate but hairs originating on inner surface of calyx        |
| Inflorescence            | heads solitary, racemose or paniculate  | heads solitary or occasionally racemose   | heads solitary or paniculate   |
| Habit                    | low, rhizomatous, spreading, mat-forming  | low, rhizomatous, spreading, mat-forming  | upright sub-shrub, branched above, woody at base                         |
| Habitat Range            | alpine-subalpine<br>Owens Peak, Olancha Peak, to Little Cottonwood Creek, eastern edge of southern Sierran Crest, Kern, Inyo, and Tulare counties, CA | alpine-subalpine<br>highest peaks of San Gabriel Mtns., Los Angeles and San Bernardino counties, CA | desert montane<br>Maricopa, Mojave, Pima, Yavapai, and Yuma counties, AZ |



two species, however, are morphologically very distinct from *M. beneolens* in their more tightly clumped habit; absent or inconspicuous tightly appressed non-glandular vestiture; and narrow, petiolate, punctate leaves.

Instead, the most similar species is *M. cinerea* Abrams, from subalpine and alpine habitats in the San Gabriel Mountains of southern California. Both geographically restricted species form openly rhizomatous mats in scree and have subsessile ovate leaves, but *M. cinerea* lacks the undulate leaf margins and some vestiture characteristics of *M. beneolens* (Table 1). Habit, vestiture, leaf and inflorescence characteristics also allow a comparison with *M. arizonica* Epling, an endemic of Arizona desert ranges, as summarized in Table 1.

*Monardella beneolens* also has striking similarities in vestiture, leaf form, and habit with two coastal dune species of central California which have been called *M. crispa* Elmer and *M. undulata* Benth. var. *frutescens* Hoover (Hoover 1949; Munz 1968; Smith 1976). *Monardella beneolens* and these dune taxa share scarious lavender to rose colored bracts and undulate leaf margins. They flourish on unconsolidated, shifting mineral substrates and one coastal form has a low, rhizomatous mat-forming habit. Although *M. beneolens* and the dune taxa are geographically and elevationally widely separated, their shared morphological traits are nonetheless intriguing.

Two other geographically restricted species that share spreading glandular and eglandular villous hairs in flowering heads and characteristics of bract texture and arrangement are *Monardella robisonii* Epling in Munz and an undescribed *Monardella* (Hardham and Bartel submitted for publ.). These numerous possible relatives argue against assigning other than tentative relationships without conducting a broader and more detailed survey of *Monardella* species.

*Rarity status.* *Monardella beneolens* is highly restricted within its narrow range, occurring at three small, discrete populations along the crest of the southern Sierra Nevada. All reported populations occur on federal lands administered by either the Bureau of Land Management-California Desert Conservation Area or the United States Forest Service-Inyo National Forest. Due to the limited access and extremely arid and rugged terrain, this rare endemic is not likely to be adversely impacted by humans. Two of the populations are within the Golden Trout Wilderness, and the Owens Peak occurrence is in an area being recommended to Congress for wilderness designation by the BLM. We anticipate that more populations will be discovered as field work continues along the rugged, isolated crest of the southern Sierra Nevada.



## ACKNOWLEDGMENTS

We thank Clare Hardham for her insights into the genus, and our colleagues Mark Bagley, Steve Boyd, Dave Bramlet, Ginny Dains, Tom Daniel, Bob Holland, Dale McNeal, Jim Morefield, and Larry Norris who made the 1986 First Inter-Institutional Haybaling Expedition a success. Special thanks go to Geraldine Allen for securing the chromosome count. We are also most appreciative for the excellent illustration provided by Linda Vorobik. The authors also thank the reviewers for ways to improve the manuscript.

## LITERATURE CITED

- EPLING, C. C. 1925. Monograph of the genus *Monardella*. Ann. Missouri Bot. Gard. 12:1–106.
- HARDHAM, C. B. 1966. Three diploid species of the *Monardella villosa* complex. Leaflet. West. Bot. 16:320–326.
- HOOVER, R. F. 1949. Notes on *Monardella*. Leaflet. West. Bot. 5:179–182.
- MUNZ, P. A. 1968. A California flora and supplement. Univ. California Press, Berkeley.
- SMITH, C. F. 1976. A flora of the Santa Barbara region, California. Santa Barbara Mus. Nat. Hist.
- TATUM, J. W. 1979. The vegetation and flora of Olancho Peak, southern Sierra Nevada, California. M.A. thesis. Univ. California, Santa Barbara. 304 pp.

(Received 30 Jan 1989; revision accepted 28 Aug 1989.)

## ANNOUNCEMENT

## THIRTEENTH GRADUATE STUDENT MEETINGS

The California Botanical Society will sponsor the Thirteenth Graduate Student Meetings on Saturday, 17 March 1990, hosted by the Rancho Santa Ana Botanic Garden. Presentations will take place in the Albrecht Auditorium on the Claremont Graduate School campus.

The presentations of proposed research, research in progress, and finished research will promote exchange of ideas and information among the graduate student community. Awards in each category will be given at a banquet following the talks. All member and non-member graduate students pursuing research in plant science are invited to participate. Students not giving a paper, but with prior presentation experience, may participate as awards judges.

Abstracts are due on 20 February 1990. For further registration information contact James D. Morefield, Graduate Student Representative, Rancho Santa Ana Botanic Garden, 1500 N. College Ave., Claremont, CA 91711-3101.



## NOTES

THE TAXONOMIC RELATIONSHIPS OF *ALLOCARYA CORALLICARPA* (BORAGINACEAE).—In western Oregon, two species of *Plagiobothrys* are distinctive in having relatively showy flowers, in which the corolla limb is 5–10 mm broad. One, *P. figuratus* (Piper) I. M. Johnston, is common and widespread (southern Vancouver Island to southwestern Oregon), whereas the other, *P. hirtus* (E. Greene) I. M. Johnston, exists only in a small area of Douglas County, near the towns of Sutherlin and Yoncalla. *Plagiobothrys hirtus* is under consideration by the Oregon Department of Agriculture for possible listing and protection under the state's endangered species regulations. It is also included, under the name *P. hirtus* var. *hirtus*, on the federal list of candidate species (C2 designation) of the U.S. Fish and Wildlife Service, Endangered Species Office. Although *P. hirtus* is similar to *P. figuratus* in the morphology of the corolla and nutlets, the two species consistently differ in the pubescence of the upper stems and branches, which are strigose in *P. figuratus* and spreading hirsute in *P. hirtus* (see A. Cronquist in C. L. Hitchcock et al., Vasc. Pl. Pac. N.W. 4:239, 1959). In Douglas County, *P. figuratus* sometimes grows sympatrically with *P. hirtus* (e.g., J. Kagan 6038302, 6038303, Hwy. 99 just south of the I-5 exit to Sutherlin; ORE). No plants have been seen that combine the distinctive pubescence types of the two taxa. Cronquist (loc. cit.) at one time suggested that the two species might have to be united taxonomically, but their ability to remain biologically distinct when sympatric makes such a merger unnecessary.

This note is to comment on a third related taxon, designated on the federal C2 candidate species list as *P. hirtus* var. *corallicarpus* (Piper) I. M. Johnston. I have examined type specimens of the basionym *Allocarya corallicarpa* Piper (C. V. Piper 5021, Grants Pass, Josephine Co., US [holotype], GH, WS [isotypes]; C. V. Piper 5022, Medford, Jackson Co., GH, WS [paratypes]; M. E. Peck 2956, Grants Pass, WILLU, WS [paratypes]), and all available specimens of *P. hirtus* and *P. figuratus* at OSC and ORE. In Piper's original publication (Proc. Biol. Soc. Wash. 37:93–94, 1924), the stems of *A. corallicarpa* are described as “strigillose,” and this can be verified on the type specimens, which show the same dense and rather fine, appressed trichomes as occur in *P. figuratus*. In other traits, such as leaf pubescence, corolla size, and bractless, geminate racemes, *A. corallicarpa* strongly resembles *P. figuratus* as well. The type specimens of *A. corallicarpa* possess nutlets that are more prominently ridged, and hence more deeply alveolate, than in *P. figuratus* and *P. hirtus*. Variation in the shape and size of the nutlets, as well as characteristics of the attachment-scar, are otherwise similar in all three taxa.

In the taxonomically important trait of stem pubescence, *A. corallicarpa* resembles *P. figuratus* rather than *P. hirtus*. Why, then, did I. M. Johnston make it a variety of the latter species rather than the former? At the time he published the combination *P. hirtus* var. *corallicarpus* (J. Arnold Arb. 16:193, 1935), Johnston considered the three taxa under discussion—*hirtus*, *figuratus*, and *corallicarpus*—to be conspecific. Because the epithet *hirtus*, based on *Allocarya hirta* Greene (Pittonia 1:161, 1888) had priority, Johnston adopted it in making his new combinations in *Plagiobothrys*, and reduced *figuratus* and *corallicarpus* to varietal rank. By taking up the name *P. hirtus*, Johnston was correcting his earlier view (Contr. Arnold Arb. 3:52–54, 1932) that *P. scouleri* (Hook. & Arn.) I. M. Johnston should be applied to the species containing *hirtus*, *figuratus*, and *corallicarpus*. By 1935, he had examined the original collections of *P. scouleri* at Kew and concluded that they represented a different species of the Pacific Northwest, having much smaller flowers than *P. hirtus*. Recent authors such as Cronquist (op. cit.) have followed this revised interpretation of *P. scouleri*.



In a letter to Morton E. Peck, dated 3 October 1939 (WILLU archives) Johnston wrote that he was inclined to separate "the common forms of the old *Allocarya Scouleri* aucts. (sic!)" from *P. hirtus*, and "(I)f this is done your plant of the Willamette Valley will have to be called *Allocarya figuratus* (sic!) Piper." Shortly thereafter, Peck published the combination "*Plagiobothrys figuratus* (Piper) Johnst." (Man. Higher Pl. Oreg. 609, 1941), without specifically citing Piper's basionym. However, in synonymy under three other species of *Plagiobothrys*, Peck does mention species names in *Allocarya* published by Piper. For nomenclatural stability, it seems best to follow the precedent of Cronquist (op. cit.) and other authors in considering that Peck's publication contains an adequate, though indirect, reference to a previously and effectively published description (see Art. 32.4, Internl. Code Bot. Nomencl., 1988).

I have seen no recent collections from southwestern Oregon having the deeply and complexly ridged nutlets of *A. corallcarpa*, and the taxon has been listed as possibly extinct ("Rare, Threatened and Endangered Plants and Animals of Oregon," Oreg. Natural Heritage Data Base, Portland, 1988). To facilitate reference to this interesting plant and provide an appropriate name, should it eventually be rediscovered, the following taxonomic change is proposed:

***Plagiobothrys figuratus* (Piper) I. M. Johnston ex M. E. Peck subsp. *corallicarpus* (Piper) Chambers, *comb. nov.*—*Allocarya corallicarpa* Piper, Proc. Biol. Soc. Wash. 37:93–94, 1924.—TYPE:** Oregon, Josephine Co., Grants Pass, *C. V. Piper 5021*, 2 Jun 1921 (holotype US!; isotypes, GH!, WS!).

*Additional specimens examined.* OR, Josephine Co.: Grants Pass, 16 May 1910, *A. A. Heller 10026* (GH); T37S R6W sect. 10, 27 Apr 1941, *E. P. Cliff C308* (GH); T37S R6W sect. 11, 11 May 1946, *L. E. Detling 5629* (ORE). Jackson Co.: Sams Valley, 7 Jun 1930, *L. F. Henderson 12727* (ORE).—KENTON L. CHAMBERS, Department of Botany and Plant Pathology, Oregon State University, Corvallis, OR 97331. (Received 17 Apr 1989; accepted 3 Jul 1989.)

---

COMMENTS AND NOTES ON *PORTULACA* IN CALIFORNIA.—Two species of *Portulaca* occur in California: *P. oleracea* L., without conspicuously hairy axils, and a second species with conspicuously hairy axils. The remainder of this discussion concerns only the hair axiled (pilose) species. This species has previously been reported for California (Munz, A California Fl., 1959) as *P. mundula* I. M. Johnston. Munz (A California Fl., 1959) describes *P. mundula* as having pink to purplish petals, but later he (Munz, A Fl. of Southern California, 1974) describes the petals as pink to purplish at least in age.

This species has been collected in California only four times: twice by Roos and Roos (*Roos and Roos 4951, 5900*) and twice by Thorne et al. (*Thorne et al. 48603, 53590*). Three collections (*Roos and Roos 4951, 5900; Thorne et al. 53590*) are from the same general area (Little San Bernardino Mts./Hidden Valley/Joshua Tree Nat. Mon.), and a fourth (*Thorne 48603*) from the New York Mts. All the Roos and Roos specimens note the petals as yellow, drying reddish, and are labeled *P. parvula* A. Gray. The *Roos and Roos 5900* specimen at RSA/POM is annotated "*P. mundula* ? PAM-1970" by Munz. The Thorne et al. collections do not note petal color. Apparently the Thorne collections are labeled *P. mundula* because the only pilose (hairy axiled) *Portulaca* in Munz (A California Fl., 1959; A Fl. of Southern California, 1974) is *P. mundula*. Based on the Roos and Roos material the pilose *Portulaca* species in California has yellow petals, not red.

Matthews and Levins (Castanea 50:96–104, 1985; Sida 11:45–61, 1985; Syst. Bot. 11:302–308, 1986), working on *Portulaca* in the southeast U.S., summarize problems with *Portulaca* identification, classification, and evolution. They note the need for flower color information on herbarium material and the difficulties in using capsule



and seed morphology for identification. Matthews and Levins (Sida 11:45–61, 1985) treat *P. mundula* as a synonym of *P. pilosa* L. They believe *P. pilosa* (incl. *P. mundula*) may be exclusively red flowered. This conclusion is based on studies of over 700 specimens from as far west as Texas and Oklahoma. The yellow flowered *P. parvula* species status could not be resolved by Matthews and Levins (Sida 11:45–61, 1985). Legrand (Anales Mus. Nac. Montevideo 7:1–147, 1962) treats *P. parvula* as a synonym of the yellow flowered *P. halimoides* L. Wiggins (Fl. of Baja California, 1980) separates *P. parvula* (petals yellow) from *P. halimoides* (petals yellow with white tips). To evaluate the *P. mundula* (*P. pilosa*) and *P. parvula* (*P. halimoides*) species status in the western U.S., I examined material from Baja California. Only two collections (Wiggins 15430, 15725) were found that noted petal color. The yellow flowered specimen of *P. parvula* (Wiggins 15430) was identical to the California material (Roos and Roos 4951, 5900; Thorne et al. 48603, 53590). The red flowered specimen of *P. mundula* (Wiggins 15725) fit the description of *P. pilosa* (Matthews and Levins, Sida 11:45–61, 1985).

The pilose California species is *P. parvula* which should be treated as a synonym of *P. halimoides* following Legrand (Anales Mus. Nac. Montevideo 7:1–147, 1962). *Portulaca pilosa* (synonym *P. mundula*) is not known from California. Thus in my contribution to the revision of Jepson's Manual of Plants of California, I list the pilose California *Portulaca* as *P. halimoides*. Additional studies are needed in CA, AZ, NM, and Mex to better understand the systematics and biogeography of the red flowered *P. pilosa* (*P. mundula*) and yellow flowered *P. halimoides* (*P. parvula*) in the southwest U.S.

*Specimens examined.* *Portulaca halimoides* L. USA, CA, Riverside Co.: Little San Bernardino Mts., Hidden Valley, 18 Oct 1952, Roos and Roos 5900 (RSA, CAS, DS, UC); Joshua Tree Natl. Mon., Hidden Valley, 22 Aug 1979, Thorne et al. 53590 (RSA). San Bernardino Co.: Valley Wells, eastern Mohave Desert, 1 Sep 1950, Roos and Roos 4951 (UC, CAS, DS); New York Mts., Cottonwood Springs, 29 Oct 1976, Thorne et al. 48603 (RSA). MEXICO: Baja California Sur, Cabo San Lucas, 1 Jan 1959, Wiggins 15430 (CAS, DS).

*Portulaca pilosa* L. MEXICO: Baja California Sur, SW of La Paz, 2 Dec 1959, Wiggins 15725 (CAS, DS).

I thank James F. Matthews for helpful discussion of species problems in *Portulaca*, providing reprints, and making his copy of the Legrand monograph available. The comments of Lawrence M. Kelly, an anonymous reviewer, and the editor are appreciated. Thanks also to the cited institutions for loans. — WALTER A. KELLEY, Biology Department—Herbarium, Mesa State College, Grand Junction, Co. 81501.

(Received 16 Nov 1988; revision accepted 29 Aug 1989.)

## ERRATUM

In "The *Aristida californica*-*glabrata* complex (Gramineae)" by J. R. Reeder and R. S. Felger (Madroño 36(3):187–197, 1989), the legend for Fig. 3, p. 195, should read: Elevational distribution for *Aristida californica* var. *californica* (open circles) and var. *glabrata* (solid circles).



## NOTEWORTHY COLLECTIONS

### CALIFORNIA

*WOLFFIA ARRHIZA* (L.) Horkel ex Wimmer [LEMNACEAE].—USA, CA, San Diego Co., San Dieguito River, pond at base of Lake Hodges Dam spillway (33°2'N, 117°8'W), 76 m, 4 Dec 1988, *Armstrong 1297*. Forming dense colonies at water surface with *Azolla filiculoides* and *Lemna minuscula*. Associated with *Typha latifolia*, *Ludwigia peploides* subsp. *peploides*, *Pluchea odorata* var. *odorata*, *Cyperus erythrorhizos*, and *Berula erecta*. Verified by E. Landolt 19 Dec 1988.

*Previous knowledge.* Known from Europe, SW Asia, Africa and E Brazil. A minute, free-floating rootless angiosperm, barely visible without magnification. Often associated with *Lemna*, *Spirodela*, and *Azolla*. CA collections from Oso Flaco Lake, San Luis Obispo Co., reported as *W. arrhiza* by Mason (1957), have been annotated by Landolt as *W. columbiana*. Contrary to Daubs (1965), another similar CA sp., *W. globosa* (syn. *W. cylindracea*), is not synonymous with *W. arrhiza*. All 3 spp. belong to the Section *Wolffia* and are undoubtedly closely related. The upper surface of *W. arrhiza* is dark green and conspicuously flattened, with 15–100 stomata (Fig. 1). The upper surfaces of *W. columbiana* and *W. globosa* are transparent green, generally with 1–12 stomata. Although fronds of *W. globosa* are flat-topped, they are more cylindrical and much smaller, generally only 0.4–0.7 mm long (compared with 0.8–1.3 mm for *W. arrhiza*). The other conspicuously flat topped sp. in N. Amer., *W. borealis*, is occasionally misidentified as *W. arrhiza*. It can readily be distinguished by its brown pigment cells, visible on dead plants. (Herbaria consulted: RSA, SD, UC, ZT; published sources: Landolt, Veröff. Geobot. Inst. ETH 71. 1986; Armstrong and Thorne, Madroño 31:172–179, 1984; Daubs, Ill. Biol. Monogr. 34, 1965).

*Significance.* First authenticated record of *W. arrhiza* in N. Amer. This population is probably naturalized due to its close proximity to a nearby biological supply company. Readily introduced through fish and aquarium cultures, it is to be expected elsewhere in CA. Because of variable frond characteristics it is easily mistaken for the native *W. columbiana*.

*WOLFFIA BRASILIENSIS* Weddell [LEMNACEAE].—USA, CA, Butte Co., Sacramento River, Chico Landing Ramp (at Chico Landing Site), Bidwell River Park w. of Chico (39°43'N, 121°56'W), 30 m, 6 Nov 1988, *Oswald 3723*. Scattered individuals in shallow slough in an old channel of the Sacramento River. Associated with a dense population of *Lemna turionifera* and *L. minuscula*. Verified by E. Landolt 30 Nov 1988.

*Previous knowledge.* Known from E and SE US, the Caribbean region, C. and S. Amer. A minute, free-floating rootless angiosperm, barely visible without magnification. Often associated with *Lemna*, *Spirodela*, *Wolffiella*, and *Azolla*. Distinguished from all other *Wolffia* spp. by prominent conical papule in center of upper surface (Fig. 2). This species and *W. borealis* belong to the Section *Pigmentatae*. Dead plants of both spp. are dotted (punctate) with brown pigment cells. The pigment is a phlobaphene-like substance formed by oxidation and polymerization of phenolic compounds when the plant dies. The upper surface of both spp. is dark green, conspicuously pitted with numerous stomata. The lower, submersed surface is transparent green. Commonly published synonyms for *W. brasiliensis* are *W. papulifera* Thompson and *W. punctata* Grisebach. The *W. punctata* of some American authors (not Grisebach) refers to *W. borealis*. The confusion between the two spp. apparently originated from the type specimen of *W. brasiliensis* which did not show the typical dorsal papule. (Herbaria consulted: RSA, SD, UC, ZT; published sources: Landolt,



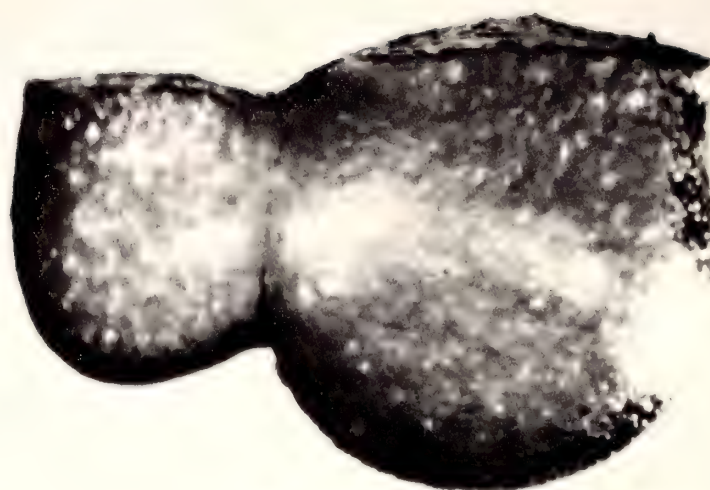
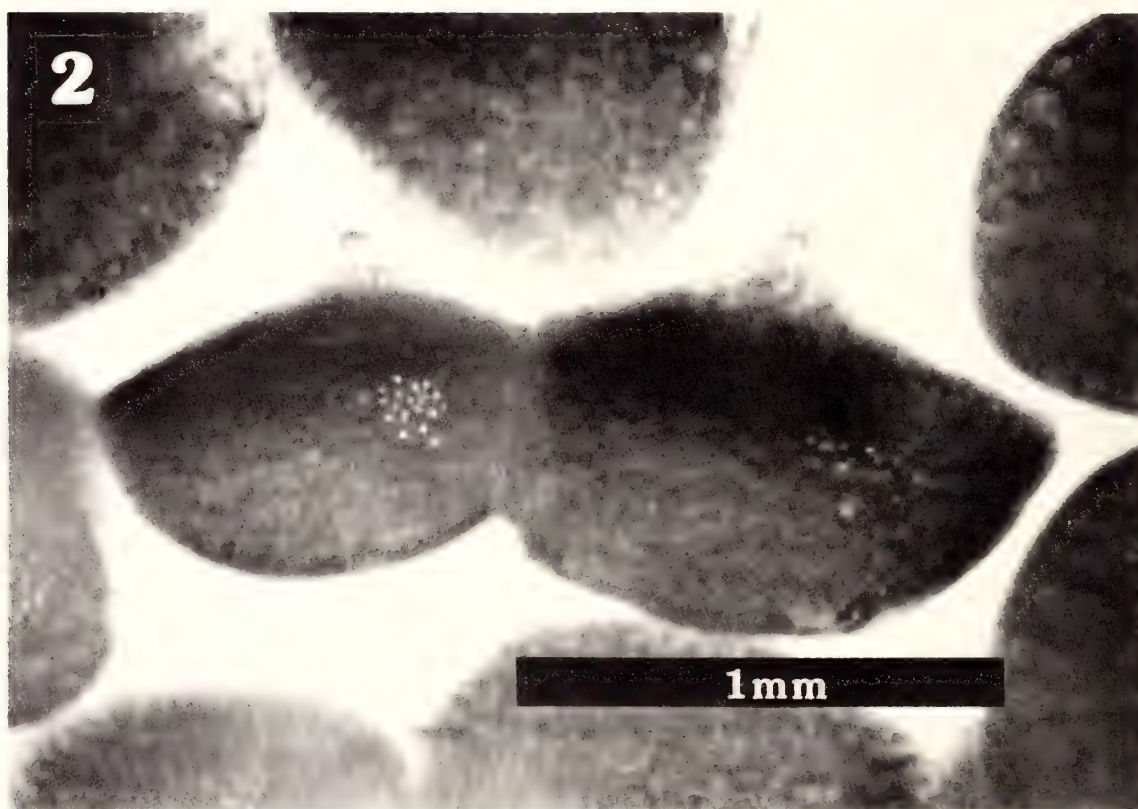
**1****1mm****2****1mm**

FIG. 1. Lateral view of budding *Wolffia arrhiza* showing the conspicuously flattened dorsal surface.

FIG. 2. Lateral view of budding *Wolffia brasiliensis* showing conspicuous dorsal papule.



Veröff. Geobot. Inst. ETH 71. 1986; Armstrong and Thorne, Madroño 31:172–179, 1984).

*Significance.* First record of *W. brasiliensis* in CA, a NW extension of 2400 km from the Gualalupe River near Hunt, Texas, Kerr Co. Small and flowering plants without a central papule are easily mistaken for *W. borealis*. Since papules are not always visible in herbarium samples, it is recommended that dried fronds be boiled in order to obtain typical shape. The pointed, upturned apex of *W. borealis* is also more easily recognizable in boiled specimens.

Five native and naturalized spp. of *Wolffia* are now known from CA: *W. brasiliensis*, *W. borealis*, *W. columbiana*, *W. globosa*, and *W. arrhiza*. —WAYNE P. ARMSTRONG, Palomar College, San Marcos, CA 92069.

#### COLORADO

*ENNAEPOGON DESVAUXII* Beauv. (POACEAE). — Montrose Co., sandy soil in slick rock areas, Sewemup Mesa (T49N R18W sect. 33, 38°30'N, 109°55'W), 1750 m, 19 Sept 1987, *Kelley and Ballard 87-106A* (Mesa State College Herb., CS).

*Previous knowledge.* On dry sandy soil on open desert flats in CA, AZ, NM, TX, Mex, and S. Am.

*Significance.* First record for this species in CO, representing a range extension eastward from nearest known localities in Grand Co., UT (Welsh et al., Great Basin Nat Memoirs 9:729, 1987).

*ERAGROSTIS SPECTABILIS* (Pursh) Steudel (POACEAE). — Montrose Co., sandy soil in slick rock areas, Sewemup Mesa (T49N R18W sect. 33, 38°30'N, 109°55'W), 1750 m, 26 Aug 1987, *Kelley 87-104* (Mesa State College Herb., CS) (verified by Ronald L. Hartman).

*Previous knowledge.* Sandy soil ME to MN and ND, S to FL and AZ, also W.I. and E Mex.

*Significance.* First record for this species in the Great Basin.

*LYCURUS PHLEOIDES* Kunth (POACEAE). — Montrose Co., sandy soil in slick rock areas, Sewemup Mesa (T49N R18W sect. 33, 38°30'N, 109°55'W), 1750 m, 26 Aug 1987, *Kelley 87-103* (Mesa State College Herb., CS).

*Previous knowledge.* Sandy soil E CO, SW KS, S to TX, AZ, NM, Mex, S UT.

*Significance.* Although common in the eastern plains of CO, this is the first record of the species in W CO, representing a range extension NE from known localities in S UT.

*PHACELIA CONSTANCEI* Atw. (HYDROPHYLLACEAE). — Mesa Co., NE-facing slopes in gypsum soils, NW corner of Sinbad Valley (T49N R19W sect. 5, 38°33'N, 109°02'W), 1750 m, 29 Nov 1987, *Kelley and Ballard 87-127* (Mesa State College Herb.).

*Previous knowledge.* Common on soils derived from Moenkopi formation in SE UT and NE AZ. In CO previously known only from Gypsum Gap, San Miguel Co. (38°02'N, 108°39'W).

*Significance.* This represents a second locality for this relatively rare species in CO and is a range extension of 80km NNW of Gypsum Gap.

*POLIOMINTHA INCANA* (Torrey) A. Gray (LAMIACEAE). — Montezuma Co., near state line east of Aneth, [UT] on sandy soil (37°30'N, 109°00'W), 1830 m, 19 Jun 1968, *Harrington 10107* (CS).

*Previous knowledge.* On sandy soil in SE UT, NC and E AZ, NM, W TX, and Chihuahua, Mex.

*Significance.* First record for CO and range extension immediately E from adjacent populations in San Juan Co., UT.



*POLYSTICHUM SCOPULINUM* (D. Eaton) Maxon (ASPIDIACEAE). — Moffat Co., east side of Cross Mountain Canyon (T6N R98W sect. 1), 1890 m, 16 Sept 1983, *J. C. Parks* 914.

*Significance.* First CO report of this species and an extension of ca. 270 km E of the nearest known site in Salt Lake Co., UT. — WALT KELLEY, Department of Biology, Mesa State College, Grand Junction, CO 81501 and DIETER H. WILKEN, Department of Biology, Colorado State University, Fort Collins, CO 80523.

## ANNOUNCEMENT

### NEW PUBLICATIONS

MICKEL, J. T. and J. M. BEITEL, Pteridophyte flora of Oaxaca, Mexico, *Memoirs of the New York Botanical Garden*, Vol. 46, pp. [i-ii], 1-568, 15 July 1988, ISSN 0071-5794, ISBN 0-89327-323-6, \$94.85 U.S., \$96.80 foreign, postpaid (from Scientific Publications Office, The New York Botanical Garden, Bronx, NY 10458-5126). [For review see R. G. Stolze, *Taxon* 38:446-447.]

PHILLIPS, R. C., and E. G. MEÑEZ, Seagrasses, *Smithsonian Contributions to the Marine Sciences*, no. 34, pp. i-v-[vi], 1-104, 1988, ISSN 0196-0768 (for price and address see entry for Funk and Mori). [On all known taxa of seagrasses (12 gen., 48 spp.), with keys, 4 tables, 57 figs., 39 maps, 5-p. biblio. summarizing general and current info on morphology, ecology, biology, distribution, and evolution.]

RICKETTS, E. F., J. CALVIN and J. W. HEDGPETH, *Between Pacific tides*, 5th ed., rev. by D. W. Phillips, Stanford University Press, Stanford, CA 94305, 1985, xxvi, [i], 652 pp., illus., ISBN 0-8047-1229-8, \$29.50, ISBN 0-8047-1244-1, \$22.00 (both hardbound). [Previous eds. 1939, 1948, 1952, 1962, 1968; a major revision of Rickett's (1896-1948) classic. The less expensive version is a recently issued ocean manual with the dust jacket built into a plasticized cover.]

ROWLEY, G. D., *Caudiciform & pachycaul succulents: Pachycauls, bottle-, barrel- and elephant-trees and their kin: A collector's miscellany*, Strawberry Press, 227 Strawberry Dr., Mill Valley, CA 94941, 1987, xiii, [i], 282 pp., illus. (most color), endpaper photos, ISBN 0-912647-03-5 (hardbound), \$65.00. [With superb photos of various desert plants. For review see R. Schmid, *Taxon* 38:450.]

RUSHFORTH, K. D., *Conifers*, Facts on File Publications, 460 Park Ave. S., New York, NY 10016, 1987, 232 pp., 8 pls. (color), text illus. (B&W), ISBN 0-8160-1735-2 (hardbound), \$24.95. [Publ. in Britain by Christopher Helm, Bromley. With much on cultivation and a 148-page gazetteer for nearly 600 spp. For review see J. A. Weber, *Michigan Bot.* 27:95.]



## REVIEWS

*Baja California Plant Field Guide.* By NORMAN C. ROBERTS Natural History Publishing Company, P.O. Box 962, La Jolla, CA 92037. 1989. xv + 309 pp. \$22.95 plus \$2.00 postage and handling.

This long-anticipated successor to the out-of-print *A Field Guide to the Common and Interesting Plants of Baja California* by Coyle and Roberts is a third larger. Items criticized in the earlier work have been meticulously eliminated.

After initial division into gymnosperms, angiosperms, monocots and dicots, arrangement of the families, and of genera within families, is alphabetical. Most users will undoubtedly find this arrangement preferable to the systematic arrangement of the previous work. The quality of the photographs for the more than 275 species illustrated is excellent. Oftentimes, habit photos are included as well as close-ups of flower and fruit. Although this volume treats only about one-tenth of the plants included in Wiggins' *Flora of Baja California*, those species most apt to be noticed by travellers are included. Because the same vernacular name is sometimes applied to more than one plant, there is occasionally a problem in matching photos with text. In one unfortunate incident (p. 87) the titles for "Sotol" and "Lechuguilla" are reversed. The comparative full page plates for species of *Cercidium*, *Acacia*, and *Prosopis* are most useful. Expanded ethnobotanical information is most welcome.

Introductory material provides travellers with valuable and interesting information regarding such subjects as physical geography, geology, diverse climate, endemism, and phytogeographic areas. The section treating the Cape Region might be less confusing to the uninitiated if discussion were confined to the geographic Cape Region south of the isthmus of La Paz. Here, the mountains are granitic, instead of volcanic as in the Sierra de la Giganta to the north. Roberts' inclusion of the latter in the Cape Region area is made on the basis of the vegetational classification proposed by Shreve and Wiggins. During early geologic periods the Cape Region mountains remained as an island when all but the higher peaks about as far north as Lat. 28°N were submerged. Furthermore, according to the Plate theory, before its separation from mainland Mexico, what was to become the peninsula, was attached to the mainland much farther south. This may serve to explain the presence in the Cape Region mountains of some more southerly mainland elements. Shrubby *Hybanthus mexicanus* is an example. As in the previous *Guide*, the illustrated glossary is useful, as is the expanded glossary of botanical terms and Spanish words. Unfortunately, the illustration of spike (p. 69) does not clearly conform to the definition. Roberts includes in his Bibliography Miguel del Barco's important contribution to our knowledge of the natural history of the peninsula. However, he does not mention the fact that English translations of two important sections of Barco's book have been published by Glen Dawson.

"Aficionados" of Baja California, as well as new travellers, will warmly welcome Norman Roberts' contribution as an aid to their appreciation of this fascinating peninsula.—ANNETTA CARTER, University Herbarium, University of California, Berkeley, CA 94720.

*The Biogeography of Fire in the San Bernardino Mountains of California—A Historical Study.* By RICHARD A. MINNICH. University of California Publications in Geography Volume 28, University of California Press, Berkeley. 120 pp. plus plates, soft cover.

This modest size book (74 pp. text) deals with more than the ecology of wildfires. Half of the pages are devoted to a historical account of the biogeography of plant



communities in this eastern-most section of the southern Californian Transverse Range. Minnich provides a fascinating description of the anthropogenic impact on the ecology of plant communities in this region. The thoroughness of the library research behind this history is suggested by the countless references to relatively obscure documents and the >60 pages of tables, figures and appendices.

Although this historical account of the San Bernardino Mountain Region could stand alone, it is laid out here to provide a backdrop for Minnich's thesis on the ecological impact of 20th century fire suppression. Briefly, the thesis is that although humans ignite as well as suppress most wildfires, it is the latter activity which has most dramatically affected the contemporary landscape. As this paradigm dominates modern forestry management, it should be well received by many. Professor Minnich uses historical accounts of wildfires to support the hypothesis that prior to fire suppression there were always sufficient fire ignitions to produce conflagrations whenever fuel loads were suitable for fire spread. Due to the inherent characteristics of historical documents, they leave much to the reader's imagination and provide fertile ground for speculation. The author takes full advantage although there is an inordinate use of the word "probably" throughout the latter half of the book. Minnich does an admirable job piecing together a cogent story from many disparate pieces of information though in some instances the author was too quick to dispatch data contrary to his thesis. For example, authors in the early part of the 20th century commented that the range of bigcone spruce was shrinking due to increasing frequency of anthropogenic fire ignitions. As this conflicts with the thesis, Minnich suggested, without much evidence, that botanists such as Sudworth, Jaeger and others had a poor grasp of the biology of this tree.

Occasionally the author uses physical geography jargon that may be unfamiliar to some readers, but in context it does not present an obstacle to those of us unfamiliar with such terminology. This is a very readable book from which both students and professionals will benefit.—JON E. KEELEY, Department of Biology, Occidental College, Los Angeles, CA 90041.

## ANNOUNCEMENT

### NEW PUBLICATION

VITT, D. H., J. E. MARSH and R. B. BOVEY, *Mosses, lichens & ferns of northwest North America: A photographic field guide*, Lone Pine Publishing, 414, 10357 109th St., Edmonton, Alberta T5J 1N3, Canada, 1988, 296 pp., illus. (B&W, color), ISBN 0-919433-41-3 (paperbound), US\$17.50. [Subtitle on cover only, not on t.p. On 374 spp. (170 spp. mosses, 20 liverworts, 156 lichens, 28 pteridophytes), about 15% of the total cryptogram land flora, each species with map and color photo.]

SUNSET BOOKS and *Sunset Magazine* (eds.), *Sunset western garden book*, 6th ed., Land Publishing Co., Menlo Park, CA, fall 1988, 592 pp., illus. (91 pp. color), ISBN 0-376-03853-5 (hardbound), \$22.95, ISBN 0-376-03891-8 (paperbound), \$16.95 (from Sunset Books, P.O. Box 10686, Des Moines, IA 50380-0686). [Previous eds. 1933, 1937, 1954, 1967, 1979, but present work inexplicably called a "fifth edition". With listings for over 6000 species. Emphasis is on western N. America, but due to much of its Mediterranean and xeric climate, the book has considerable relevance to other areas of water stress.]



## EDITOR'S REPORT FOR VOLUME 36

This annual report provides an opportunity for the editor to communicate the status of manuscripts received for publication in *Madroño* and to comment on other aspects of the journal. Between 1 July 1988 and 30 June 1989, 58 manuscripts were received (31 articles, 14 notes, and 13 noteworthy collections contributions totalling 32 individual taxa). Since 30 June 1989, 11 manuscripts have been received (9, 0, 2). The current status of the 36 unpublished manuscripts is 5 in review (5, 0, 0), 20 in revision (15, 5, 2), 0 needing decision by the editor, and 11 accepted for publication (7, 1, 3). Volume 36 included 60 published manuscripts (25, 10, 11, 2), 9 book reviews, and 3 commentaries. The period between submittal and publication averaged 11–12 months for articles. Three manuscripts (2, 1, 0) were rejected. Sixteen manuscripts (13, 1, 2) that were returned well over one year ago to the authors for revision are considered to have been withdrawn.

Several individuals have been of much help to me as Editor. I much appreciate the efforts of members of the Editorial Board. Steven Timbrook has once again prepared the annual Index and Table of Contents, and Rudolf Schmid has prepared announcements and reviews of new publications.

My thanks also go to the authors whose papers I have edited for their patience and willingness to respond to my comments and those of the reviewers.

Articles and notes in *Madroño* continue to reflect the wide-ranging interests of members of the California Botanical Society. Topics discussed in volume 36 include cytology, ecology, floristics, hybridization, nomenclature, phytogeography, and systematics. The papers represent geographical areas from Canada, various areas of the United States, Mexico, and Costa Rica. *Madroño* continues to serve as a source of additional information through reviews, commentaries, and announcements that inform members of the Society of publications, meetings, and other topics of interest. As Editor, I encourage potential authors to continue to submit manuscripts that maintain the broad cross-section of botanical topics.—D.J.K. 20 Nov 1989.

### ANNOUNCEMENT

#### NEW PUBLICATION

SAUER, J. D., *Plant migration: The dynamics of geographic patterning in seed plant species*, University of California Press, 2120 Berkeley Way, Berkeley, CA 94720, 1988, xvi, 282 pp., illus., ISBN 0-520-06003-2 (hardbound), \$45.00. [Detailed discussions of many cases worldwide, with much on California (e.g., naturalization of *Avicennia*, *Mesembryanthemum*, and other exotics) and western North America. For reviews see G. T. Prance, *BioScience* 38:804, and R. Schmid, *Taxon* 38:450–451.]

TAYLOR, N. P., *The genus Echinocereus*, Timber Press, 9999 SW. Wilshire, Portland, OR 97225, 1985, 160 pp., 12 pls. (color), text illus. (B&W), ISBN 0-88192-052-5 (hardbound), \$27.95. [Publ. in Britain by Collingridge Books, Twickenham. *A Kew Magazine monograph* (unnum.). On the taxonomy of 44 spp. in 8 sect.]



## REVIEWERS OF MANUSCRIPTS

As Editor, I thank all reviewers for their assistance with manuscripts. Special thanks are extended to those who reviewed several manuscripts published in 1989. I am very grateful to each reviewer for his or her generous contribution of time and effort. The quality of papers published in Madroño reflects this contribution. Reviewers for volume 36 are:

|                         |                      |                        |
|-------------------------|----------------------|------------------------|
| George W. Argus         | Larry C. Higgins     | Bruce D. Parfitt       |
| Mary E. Barkworth       | Peter C. Hoch        | Robert W. Patterson    |
| Rupert C. Barneby       | V. L. Holland        | Richard A. Pimentel    |
| James W. Bartolome      | Duane Isely          | Donald J. Pinkava      |
| R. Mitchel Beauchamp    | S. K. Jain           | James S. Pringle       |
| Mark Borchert           | T. D. Jacobsen       | Rhonda L. Riggins      |
| Dennis E. Breedlove     | Peter T. Jankay      | Aryan I. Roest         |
| Charles L. Burandt, Jr. | Daniel H. Janzen     | Reed C. Rollins        |
| Annetta Carter          | B. M. Kapoor         | Barbara A. Schaal      |
| Adolf Ceska             | Jon E. Keeley        | Rudolf Schmid          |
| Kenton L. Chambers      | Walter A. Kelley     | John C. Semple         |
| Curtis Clark            | Lawrence Kelly       | Steven H. Sharrow      |
| Lincoln Constance       | Arthur R. Kruckeberg | Paul C. Silva          |
| Richard T. Corlett      | Meredith A. Lane     | Allen R. Smith         |
| Thomas F. Daniel        | F. Harlan Lewis      | Richard W. Spellenberg |
| Frank W. Davis          | Lazarus W. Macior    | G. Ledyard Stebbins    |
| James R. Ehleringer     | Mary Ann Matthews    | John L. Strother       |
| Barbara Ertter          | Elizabeth McClintock | Scott Sundberg         |
| Richard L. Everett      | Malcolm G. McLeod    | Barry D. Tanowitz      |
| Wayne R. Ferren, Jr.    | Dale W. McNeal, Jr.  | Ronald J. Taylor       |
| Vicki A. Funk           | Timothy Messick      | David Thompson         |
| Alwyn Gentry            | James S. Miller      | Robert A. Thorne       |
| Jeffrey Glazner         | Richard Minnich      | Frederick H. Utech     |
| William L. Halvorson    | Reid Moran           | Frank C. Vasek         |
| Clare B. Hardham        | James D. Morefield   | Jennifer von Reis      |
| Stephen Hatch           | Thomas H. Nash       | Dieter H. Wilken       |
| Frank Hawksworth        | Guy L. Nesom         | George A. Yatskievych  |
| Lawrence R. Heckard     | Lorin I. Nevling     | Helen Young            |
| James Henrickson        | Daniel L. Nickrent   |                        |

## DATES OF PUBLICATION OF MADROÑO, VOLUME 36

- Number 1, pages 1–60, published 3 May 1989
- Number 2, pages 61–140, published 11 October 1989
- Number 3, pages 141–220, published 17 October 1989
- Number 4, pages 221–288, published 25 January 1990



## INDEX TO VOLUME 36

Classified entries: major subjects, key words, and results; botanical names (new names are in **boldface**); geographical areas; reviews, commentaries. Incidental references to taxa (including most lists and tables) are not indexed separately. Species appearing in Noteworthy Collections are indexed under name, family, and state or country. Authors and titles are listed alphabetically by author in the Table of Contents to the volume.

Acanthaceae (see *Siphonoglossa*).

Alliaceae (see *Allium*).

*Allium*: New combinations, **A. jepsonii**, 127, and **A. tuolumnense**, 128; revision of *A. sanbornii* complex, 122.

*Allocarya* (also see *Plagiobothrys*): Taxonomic relationships of *A. corallicarpa*, 280.

*Antennaria*: *A. aromatica* and *A. densifolia*, systematics and phytogeography, 248.

*Aristida californica*–*glabrata* complex, systematics of, 187.

Arizona: Noteworthy collections: *Ephedra funerea*, *Melica imperfecta*, 136.

Ascomycotina: Lecanorales (see *Cladonia*).

Aspidiaceae (see *Polystichum*).

Asteraceae: *Antennaria aromatica* and *A. densifolia*, systematics and phytogeography, 248; *Encelia densifolia*, reduction in light reflectance by trichome wetting, 180; *Rudbeckia occidentalis* var. *montana*, noteworthy collection from OR, 53.

New species: **Erigeron acomanus**, 115.

*Astragalus curvicaupus* var. *subglaber*, noteworthy collection from OR, 53.

*Bealia mexicana*, taxonomy of, 260.

Boraginaceae: *Allocarya corallicarpa*, taxonomic relationships, 280; **Macromeria alba**, new species from Mexico, 28; *Myosotis latifolia* and not *M. sylvatica* in CA, 131; **Plagiobothrys figuratus** subsp. **corallicarpus**, new combination, 281.

*Botrychium* in the Jonesville area, CA, 131.

Brassicaceae (see *Streptanthus*).

Cactaceae (see *Opuntia*).

California: *Botrychium* in the Jonesville area, 131; *Cladonia*, phytogeographic notes on acidophilous species, 169; ef-

fects of fire on annual grasslands in the Sierra Nevada, 154; *Gilia maculata* taxonomic relationships, 15; *Myosotis latifolia* and not *M. sylvatica*, 131; range of *Phacelia vallicola*, 51; *Portulaca*, notes on, 281; *Quercus douglasii*, effect on herbaceous understory along a rainfall gradient, 141.

New taxa and combinations (also see *Limnanthes*): **Allium jepsonii**, 127, and **A. tuolumnense**, 128; **Hastingsia serpentinicola**, 208; **Monardella beneolens**, 271; **Streptanthus brachiatatus** subsp. **hoffmanii**, 36, and **S. morisonii** subsp. **kruckebergii**, 39.

Noteworthy collections: *Pallavicinia lyellii*, *Penstemon venustus*, 53; *Polygonum marinense*, 207; *Prunus fasciculata* var. *fasciculata*, 32; *Wolffia arrhiza* and *W. brasiliensis*, 283.

*Calycolpus*: revised generic description, 9; **C. alternifolius**, new combination, 10; *Myrtus alternifolius* transferred to, 9.

Canada: British Columbia: Noteworthy collection of *Wolffia columbiana*, 153.

Chromosome numbers: *Antennaria aromatica* and *A. densifolia*, 248; *Aristida californica*, 187; North American *Lathyrus*, 41.

*Cladonia*, phytogeographic notes on acidophilous species in CA, 169.

*Clarkia*, floral pigmentation patterns, 1.

*Collomia debilis* var. *larsenii*, noteworthy collection from OR, 53.

Colorado: Noteworthy collections of *Ennaepogon desvauxii*, *Eragrostis spectabilis*, *Lycurus phleoides*, *Phacelia constancei*, *Poliomintha incana*, and *Polystichum scopulinum*, 285.

Compositae (see Asteraceae).

Costa Rica: Postfire vegetation development in paramos, 93; **Siphonoglossa ramosa** var. **hondurensis**, new combination from Costa Rica and Honduras, 205.

Cruciferae (see Brassicaceae).



**Daphnopsis lagunae**, new species from Mexico, 267.

Douglas, David, commentary on in author citations of new Jepson's flora, 137; rebuttal, 218.

*Encelia densifolia*, reduction in light reflectance by trichome wetting, 180.

*Ephedra funerea*, noteworthy collection from AZ, 136.

Ephedraceae (see *Ephedra*).

**Erigeron acomanus**, new species from NM, 115.

Fabaceae: *Astragalus curvicaupus* var. *subglaber*, noteworthy collection from OR, 53; chromosome numbers of North American *Lathyrus*, 41.

Fagaceae (see *Quercus*).

Fire: Effects on annual grasslands in the Sierra Nevada of CA, 154; postfire vegetation in Costa Rican paramos, 93.

Flora of Sierra de la Laguna, Baja California Sur, Mexico, 61.

Floral pigmentation patterns in *Clarkia*, 1.

*Gentiana setigera* correct name for *G. bisetata*, 49.

Gentianaceae (see *Gentiana*).

*Gilia maculata*, taxonomic relationships, 15.

*Goodyera repens*, noteworthy collection from MT, 174.

Gramineae (see Poaceae).

Grasslands, effects of fire in the Sierra Nevada of CA, 154.

Guatemala: New combination, **Siphonoglossa ramosa** var. **discolor**, 204.

**Hastingsia serpentinicola**, new species from CA and OR segregated from *H. alba*, 208.

Hepaticae: Pallaviciniaceae (see *Pallavicinia*).

Herbaceous understory, effects of *Quercus douglasii* on, 141.

Honduras: **Siphonoglossa ramosa** var. **hondurensis**, new combination from Costa Rica and Honduras, 205.

Hydrophyllaceae (see *Phacelia*).

*Isopyrum stipitatum* in the Willamette Valley, OR, 217.

Labiatae (see Lamiaceae).

Lamiaceae: **Monardella beneolens**, new species from CA, 271; *Poliomintha incana*, noteworthy collection from CO, 285.

*Lathyrus*, chromosome numbers, 41.

Leguminosae (see Fabaceae).

Lemnaceae (see *Wolffia*).

Liliaceae (see *Hastingsia*).

Limnanthaceae (see *Limnanthes*).

*Limnanthes*: New combinations, **L. alba** subsp. **versicolor**, **L. douglasii** subsp. **nivea**, **L. douglasii** subsp. **rosea**, **L. douglasii** subsp. **sulphurea**, and **L. gracilis**, 50.

**Macromeria alba**, new species from Mexico, 28.

*Melica imperfecta*, noteworthy collection from AZ, 136.

Mexico: *Bealia mexicana*, taxonomy of, 260.

Baja California Sur: *Encelia densifolia*, reduction in light reflectance by trichome wetting, 180; Sierra de la Laguna: Ecology and distribution of *Pinus lagunae* in, 84; flora of, 61.

Sonora: *Salix scouleriana*, 135.

New species: **Daphnopsis lagunae**, 267; **Macromeria alba**, 28; **Siphonoglossa mexicana**, 198.

**Monardella beneolens**, new species from CA, 271.

Montana: Noteworthy collection of *Goodyera repens*, 174.

*Myosotis latifolia* and not *M. sylvatica* in CA; 131.

Myrtaceae: *Calycolpus*, revised generic description, 9; **C. alternifolius**, new combination, 10; *Myrtus alternifolius* transferred to *Calycolpus*, 9.

*Myrtus alternifolia*, transferred to *Calycolpus*, 9.

New Mexico: **Erigeron acomanus**, new species, 115.

Onagraceae (see *Clarkia*).

Ophioglossaceae (see *Botrychium*).



- Opuntia*: **O. aggeria**, new species from TX, 226; taxonomy of *O. schottii* complex in TX, 221.
- Orchidaceae (see *Goodyera*).
- Oregon: Biosystematic studies of serpentine endemic *Phacelia capitata*, 232; *Isopyrum stipitatum* in the Willamette Valley, 217.
- New taxon and combination: **Hastingsia serpentinicola**, 208; **Plagiobothrys figuratus** subsp. **corallicarpus**, 281.
- Noteworthy collections: *Astragalus curvicaupus* var. *subglaber*, *Collomia debilis* var. *larsenii*, 53; *Panicum rigidulum*, 207; *Rudbeckia occidentalis* var. *montana*, 53.
- Pallavicinia lyellii*, noteworthy collection from CA, 53.
- Panicum rigidulum*, noteworthy collection from OR, 207.
- Paramo, postfire vegetation development in Costa Rica, 93.
- Parasitic plants (see *Phoradendron*).
- Penstemon venustus*, noteworthy collection from CA, 53.
- Phacelia*: *P. capitata*, serpentine endemic of OR, 232; *P. constancei*, noteworthy collection from CO, 285; *P. vallicola*, range of, 51.
- Phoradendron californicum*, germination and establishment, 175.
- Pinaceae (see *Pinus*).
- Pinus lagunae*, ecology and distribution in Sierra de la Laguna, Baja California Sur, Mexico, 84.
- Plagiobothrys figuratus** subsp. **corallicarpus**, new combination from OR, 281.
- Poaceae: *Aristida californica*-*glabrata* complex, systematics of, 187; *Bealia mexicana*, taxonomy of, 260.
- Noteworthy collections: *Ennaepogon desvauxii*, *Eragrostis spectabilis*, and *Lycurus phleoides* from CO, 285; *Melica imperfecta* from AZ, 136; *Panicum rigidulum* from OR, 207.
- Polemoniaceae: Noteworthy collection of *Collomia debilis* var. *larsenii* from OR, 53; taxonomic relationships of *Gilia maculata*, 15.
- Pollination biology: Floral pigmentation patterns in *Clarkia*, 1.
- Polygonaceae (see *Polygonum*).
- Polygonum marinense*, noteworthy collection from CA, 207.
- Polystichum scopulinum*, noteworthy collection from CO, 285.
- Portulaca* in CA, 281.
- Portulacaceae (see *Portulaca*).
- Prunus fasciculata* var. *fasciculata*, noteworthy collection from CA, 32.
- Quercus douglasii*, effect on herbaceous understory along a rainfall gradient, 141.
- Ranunculaceae (see *Isopyrum*).
- Reviews: Michael G. Barbour and W. Dwight Billings, eds., *North American Terrestrial Vegetation*, 219; D. W. Jeffrey, *Soil-Plant Relations: An Ecological Approach*, 219; Walter Knight with Irja Knight, *Guide to the Regional Parks Botanic Garden*, 54; K. E. Mayer and W. F. Laudenslayer, Jr., *A Guide to Wildlife Habitats of California*, 57; Richard A. Minnich, *The Biogeography of Fire in the San Bernardino Mountains of California*, 287; A. Michael Powell, *Trees and Shrubs of Trans-Pecos Texas*, 56; Norman C. Roberts, *Baja California Plant Field Guide*, 287; James P. Smith and Ken Berg, *Inventory of Rare and Endangered Vascular Plants of California*, 54; William A. Weber, *Colorado Flora: Western Slope*, 56.
- Rosaceae: *Prunus fasciculata* var. *fasciculata*, noteworthy collection from CA, 32.
- Rudbeckia occidentalis* var. *montana*, noteworthy collection from OR, 53.
- Salicaceae (see *Salix*).
- Salix*: *S. scouleriana* in Sonora, Mexico, 135; typification of *S. geyeriana*, 135.
- Scrophulariaceae (see *Penstemon*).
- Serpentine endemics (see *Allium*, *Phacelia*, and *Streptanthus*).
- Sierra de la Laguna (see Mexico).
- Sierra Nevada range: *Allium sanbornii* complex, 122; effects of fire on annual grasslands, 154; **Monardella beneolens**, new species, 271.
- Siphonoglossa*: New combinations from



Central and South America, **S. ramosa** var. **discolor**, 204, **S. ramosa** var. **hondurensis**, 205, **S. sessilis** var. **calcarea**, 198; new species from Mexico, **S. mexicana**, 198.

*Streptanthus*: New serpentine endemic subspecies from Lake County, CA, **S. brachiatus** subsp. **hoffmanii** 36, and **S. morrisonii** subsp. **kruckebergii**, 39; taxonomy of *S.* sect. *Biennis*, 33.

Texas: Taxonomy of *Opuntia schottii* complex, 221.

New species: **Opuntia aggeria**, 226.

Thymelaeaceae (see *Daphnopsis*).

Viscaceae (see *Phoradendron*).

*Wollfia*: *W. arrhiza* and *W. brasiliensis*, noteworthy collections from CA, 283; *W. columbiana*, noteworthy collection from British Columbia, Canada, 153.



## SUBSCRIPTIONS—MEMBERSHIP

Membership in the California Botanical Society is open to individuals (\$22 per year; students \$12 per year for a maximum of seven years). Members of the Society receive MADROÑO free. Family memberships (\$25) include one five-page publishing allotment and one journal. Emeritus rates are available from the Corresponding Secretary. Institutional subscriptions to MADROÑO are available (\$30). Membership is based on a calendar year only. Applications for membership (including dues), orders for subscriptions, and renewal payments should be sent to the Treasurer. Requests and rates for back issues, changes of address, and undelivered copies of MADROÑO should be sent to the Corresponding Secretary.

## INFORMATION FOR CONTRIBUTORS

Manuscripts submitted for publication in MADROÑO should be sent to the editor. All authors must be members, and membership is prerequisite for review.

Manuscripts may be submitted in English or Spanish. English-language manuscripts dealing with taxa or topics of Latin America and Spanish-language manuscripts must have a Spanish RESUMEN and an English ABSTRACT.

Manuscripts and review copies of illustrations must be submitted in triplicate for all articles and short items (NOTES, NOTEWORTHY COLLECTIONS, POINTS OF VIEW, etc.). Follow the format used in recent issues for the type of item submitted. Allow ample margins all around. Manuscripts **MUST BE DOUBLE SPACED THROUGHOUT**. For articles this includes title (all caps, centered), author names (all caps, centered), addresses (caps and lower case, centered), abstract and resumen, text, acknowledgments, literature cited, tables (caption on same page), and figure captions (grouped as consecutive paragraphs on one page). Order parts in the sequence listed, ending with figures. Each page should have a running header that includes the name(s) of the author(s), a shortened title, and the page number. Do not use a separate cover page or "erasable" paper. Avoid footnotes except to indicate address changes. Table and figure captions should contain all information relevant to information presented. All measurements and elevations should be in metric units. Specimen citations may include English or metric distance measurements.

Line copy illustrations should be clean and legible, proportioned (including captions) to the MADROÑO page, and designed for reduction to  $\frac{2}{3}$  original size. Scales should be included in figures, as should explanation of symbols, including graph coordinates. Symbols smaller than 1 mm after reduction are not acceptable. Maps must include latitude and longitude references. Halftone copy should be designed for reproduction at actual size. In no case should original illustrations be sent prior to the acceptance of a manuscript. When needed they should be mounted on stiff cardboard and sent flat. No illustrations larger than 22 × 28 cm will be accepted.

Presentation of nomenclatural matter (accepted names, synonyms, typification) should follow the format used for members of the *Allium sanbornii* complex in MADROÑO 36:124–128. 1989. Institutional abbreviations in specimen citations should follow Holmgren, Keuken, and Schofield, *Index Herbariorum*, 7th ed. Names of authors of scientific names should be abbreviated according to the Kew *Draft Index of Author Abbreviations* (1980). Abbreviation of serial titles should be those in *Botanico-Periodicum-Huntianum* (Lawrence et al., 1968, Hunt Botanical Library, Pittsburgh). If the correct abbreviation cannot be determined, the full serial title should be used. Titles of books should be given in full, together with the place and date of publication, publisher, and edition, if other than the first.

All members of the California Botanical Society are allotted five free pages per volume in MADROÑO. Joint authors may split the full page number. Beyond that number of pages a required editorial fee of \$65.00 per page will be assessed. The purpose of this fee is not to pay directly for the costs of publishing any particular paper, but rather to allow the Society to continue publishing MADROÑO on a reasonable schedule, with equity among all members for access to its pages. Printer's fees for illustrations and typographically difficult material @ \$35.00 per page (if their sum exceeds 30 percent of the paper) and for author's changes after typesetting @ \$4.50 per line will be charged to authors.

At the time of submission, authors must provide information describing the extent to which data in the manuscript have been used in other papers that are published, in press, submitted, or soon to be submitted elsewhere.





CALIFORNIA BOTANICAL SOCIETY



MADROÑO  
A WEST AMERICAN JOURNAL OF BOTANY  
VOLUME XXXVII  
1990

BOARD OF EDITORS

Class of:

- 1990—STEVEN TIMBROOK, Ganna Walska Lotusland Foundation, Montecito, CA  
THOMAS R. VAN DEVENDER, Arizona–Sonora Desert Museum, Tucson
- 1991—JAMES HENRICKSON, California State University, Los Angeles  
WAYNE R. FERREN, University of California, Santa Barbara
- 1992—BRUCE A. STEIN, The Nature Conservancy, Washington, D.C.  
WILLIAM L. HALVORSON, Channel Islands National Park, Ventura, CA
- 1993—JON E. KEELEY, Occidental College, Los Angeles, CA  
RHONDA L. RIGGINS, California Polytechnic State University, San Luis Obispo, CA
- 1994—BRUCE D. PARFITT, Arizona State University, Tempe, AZ  
PAUL H. ZEDLER, San Diego State University, San Diego, CA

*Editor*—DAVID J. KEIL  
Biological Sciences Department  
California Polytechnic State University  
San Luis Obispo, CA 93407

Published quarterly by the  
California Botanical Society, Inc.  
Life Sciences Building, University of California, Berkeley 94720

Printed by Allen Press, Inc., Lawrence, KS 66044







The 1990 volume of *Madroño* is dedicated to Herb and Florence Wagner. Herb and Florence have had a long-standing interest in West American botany which began with their Ph.D. studies at the University of California at Berkeley. Their contributions to our understanding of the biology, systematics, and evolution of ferns has been varied and of great significance. Their enthusiasm for the study of plants has been conveyed to countless students in a unique and entertaining style. They have been honored by many organizations including receiving the Asa Gray award from the American Society of Plant Taxonomists this year. Herb is one of the few botanists to become a member of the National Academy of Science.

In the year of Herb's retirement from the faculty at The University of Michigan, The California Botanical Society is pleased to honor them with this dedication.



## TABLE OF CONTENTS

|   |     |
|---|-----|
| ALLEN, GERALDINE A. (see ANTOS, JOSEPH A.)  |     |
| ALLEN, GERALDINE A. (see SHEVOCK, JAMES R., et al.)   |     |
| ALLEN, G. A., V. S. FORD, and L. D. GOTTLIEB, A new subspecies of <i>Clarkia concinna</i> (Onagraceae) from Marin County, California .....  | 305 |
| ANTOS, JOSEPH A., and GERALDINE A. ALLEN, Habitat relationships of the Pacific Coast shrub <i>Oemleria cerasiformis</i> (Rosaceae) .....  | 249 |
| AUSTIN, DANIEL F., Comments on southwestern United States <i>Evolvulus</i> and <i>Ipomoea</i> (Convolvulaceae) .....  | 124 |
| BALDWIN, BRUCE G., and DONALD W. KYHOS, A systematic and biogeographic review of <i>Raillardiopsis</i> [ <i>Raillardella</i> ] <i>muirii</i> (Asteraceae: Madiinae), with special reference to a disjunct California Coast Range population ..... | 43  |
| BARLOW, PATRICIA, Review of <i>Rare Plants of Colorado</i> by The Colorado Native Plant Society .....   | 147 |
| BARTEL, JIM A. (see SHEVOCK, JAMES R., et al.)  |     |
| BAYER, RANDALL J., A systematic study of <i>Antennaria media</i> , <i>A. pulchella</i> , and <i>A. scabra</i> (Asteraceae: Inuleae) of the Sierra Nevada and White Mountains .....  | 171 |
| BIERNER, MARK W., Present status of <i>Amblyolepis</i> (Asteraceae: Heliantheae) .  | 133 |
| BOWERS, JANICE E., William A. Cannon: The Sonoran Desert's first resident ecologist .....   | 6   |
| BRUNSFELD, STEVEN J., and FREDERIC D. JOHNSON, Cytological, morphological, ecological and phenological support for specific status of <i>Crataegus suksdorfii</i> (Rosaceae) .....  | 274 |
| DAVIS, JERROLD I., <i>Puccinellia howellii</i> (Poaceae), a new species from California   | 55  |
| DIGGS, GEORGE M., JR. (see HALL, GUSTAV W. et al.)  |     |
| DODSON, CAROLYN, Herbaria of New Mexico .....   | 311 |
| DORN, ROBERT D., <i>Thelesperma caespitosum</i> (Asteraceae), a new species from Wyoming and Utah .....   | 293 |
| DORN, ROBERT D., and ROBERT W. LICHVAR, A new variety of <i>Penstemon fremontii</i> (Scrophulariaceae) from Colorado .....  | 195 |
| FERLATTE, WILLIAM J., and JOHN L. STROTHER, <i>Potentilla cristae</i> (Rosaceae), a new species from northwestern California .....  | 190 |
| FINK, BRIAN H., and JOY B. ZEDLER, Maritime stress tolerance studies of California dune perennials .....  | 200 |
| FORD, V. S. (see ALLEN, G. A., et al.)  |     |
| GOODWIN, GREGORY A. (see SCHAAK, C. G.)   |     |
| GORDON-REEDY, PATRICIA J., Trichome patterns and geographic variation in <i>Leptodactylon californicum</i> (Polemoniaceae) .....  | 28  |
| GOTTLIEB, L. D. (see ALLEN, G. A., et al.)  |     |
| HALL, GUSTAV W., GEORGE M. DIGGS, JR., DOUGLAS E. SOLTIS, and PAMELA S. SOLTIS, Genetic uniformity of El Arbol del Tule (The Tule Tree) .....   | 1   |
| HARTMAN, RONALD L. (see SNOW, NEIL, et al.)   |     |
| HUBBARD, TERRY W. (see LARIGAUDERIE, ANNE et al.)   |     |
| JOHNSON, FREDERIC D. (see BRUNSFELD, STEVEN J.)   |     |
| KEELEY, JON E., Demographic structure of California black walnut ( <i>Juglans californica</i> ; Juglandaceae) in woodlands in southern California .....   | 37  |
| KEIL, DAVID J., Noteworthy collection of <i>Malosma laurina</i> from California ..  | 112 |
| KEIL, DAVID J., Review of <i>The Vascular Plants of Texas. A List, Updating the Manual of the Vascular Plants of Texas</i> . 2nd ed. by Marshall C. Johnston  | 314 |
| KUMMEROW, JOCHEN (see LARIGAUDERIE, ANNE et al.)  |     |
| KYHOS, DONALD W. (see BALDWIN, BRUCE G.)  |     |
| LAFERRIÈRE, JOSEPH E., and JORGE S. MARROQUÍN, <i>Berberis pimana</i> (Berberidaceae): A new species from northwestern Mexico .....   | 283 |



|   |     |
|---|-----|
| LARIGAUDERIE, ANNE, TERRY W. HUBBARD, and JOCHEN KUMMEROW, Growth dynamics of two chaparral shrub species with time after fire .....  | 225 |
| LENIHAN, JAMES M., Forest associations of Little Lost Man Creek, Humboldt County, California: Reference-level in the hierarchical structure of old-growth coastal redwood vegetation .....                        | 69  |
| LEVINSON, ALFRED (see WILSON, CAROL A. et al.)  |     |
| LICHVAR, ROBERT W. (see DORN, ROBERT D., and ROBERT W. LICHVAR)   |     |
| LISTON, AARON, Chromosome counts in <i>Astragalus</i> (Fabaceae) .....  | 59  |
| MAC, THONG (see VICKERY, ROBERT K., JR. et al.)   |     |
| MARROQUÍN, JORGE S. (see LAFERRIÈRE, JOSEPH E.)   |     |
| MASON, CHARLES T., JR., A new <i>Gentiana</i> (Gentianaceae) from northern California and southern Oregon .....   | 289 |
| MILLAR, CONNIE, Memorial for William Burke Critchfield .....  | 221 |
| MOREFIELD, JAMES D., and DEAN WM. TAYLOR, Noteworthy collections from California .....  | 64  |
| NEELY, ELIZABETH E. (see SIEMS, BARBARA A.)   |     |
| NELSON, B. E. (see SNOW, NEIL, et al.)  |     |
| O'KANE, STEVE L., JR., A new species of <i>Erigeron</i> (Asteraceae: Astereae) from Colorado .....  | 184 |
| PACK, STEVEN (see VICKERY, ROBERT K., JR. et al.)   |     |
| PETERSEN, RICHARD (see WILSON, CAROL A. et al.)   |     |
| PHILLIPS, ARTHUR M., III, Noteworthy collections from Arizona and Utah ....   | 60  |
| RAHMAN, FAHIMA (see VICKERY, ROBERT K., JR. et al.)   |     |
| RIEGEL, GREGG M., DALE A. THORNBURGH, and JOHN O. SAWYER, Forest habitat types of the South Warner Mountains, Modoc County, California .....  | 88  |
| RIGGINS, RHONDA, Review of <i>Intermountain Flora: Vascular Plants of the Intermountain West, U.S.A.</i> by Arthur Cronquist et al. Volume 3, Part B by Rupert C. Barneby .....                                   | 219 |
| SAWYER, JOHN O. (see RIEGEL, GREGG M. et al.)   |     |
| SCHILLING, EDWARD E., Taxonomic revision of <i>Viguiera</i> subg. <i>Bahiopsis</i> (Asteraceae: Heliantheae) .....  | 149 |
| SCHAACK, C. G., and GREGORY A. GOODWIN, A new subspecies of <i>Cirsium parryi</i> (Asteraceae: Cardueae) from Arizona and comments on the <i>Cirsium parryi</i> complex .....                                     | 299 |
| SHEVOCK, JAMES R., Noteworthy collections from California .....   | 62  |
| SHEVOCK, JAMES R., JIM A. BARTEL, and GERALDINE A. ALLEN, Distribution, ecology, and taxonomy of <i>Erythronium</i> (Liliaceae) in the Sierra Nevada of California .....  | 261 |
| SIEMS, BARBARA A., and ELIZABETH E. NEELY, <i>Braya glabella</i> var. <i>glabella</i> (Brassicaceae) in Colorado .....  | 145 |
| SNOW, NEIL, Noteworthy collection of <i>Chloris verticillata</i> from Wyoming .....   | 140 |
| SNOW, NEIL, B. E. NELSON, and RONALD L. HARTMAN, Additions to the vascular flora of Yellowstone National Park, Wyoming .....  | 214 |
| SOLTIS, DOUGLAS E. (see HALL, GUSTAV W. et al.)   |     |
| SOLTIS, PAMELA S. (see HALL, GUSTAV W. et al.)  |     |
| STROTHER, JOHN L. (see FERLATTE, WILLIAM J.)  |     |
| TAYLOR, DEAN WM., (see MOREFIELD, JAMES D.)   |     |
| THORNBURGH, DALE A. (see RIEGEL, GREGG M. et al.)   |     |
| VICKERY, ROBERT K., JR., FAHIMA RAHMAN, STEVEN R. PACK, and THONG MAC, Chromosome counts in section <i>Simiolus</i> of the genus <i>Mimulus</i> (Scrophulariaceae). XI. <i>M. glabratus</i> complex (cont.) ..... | 141 |
| WEST, JOHN A., Noteworthy collection of <i>Heribaudiella fluviatilis</i> from Washington .....  | 144 |
| WEST, JOHN A., and GIUSEPPE ZUCCARELLO, Noteworthy collection of <i>Caloglossa leprieurii</i> from Mexico .....   | 236 |



|   |     |
|---|-----|
| WHITTEMORE, A. T., Noteworthy collections from Mexico .....   | 217 |
| WIENS, JOHN F., Noteworthy collections from Arizona .....   | 216 |
| WILSON, CAROL A., ALFRED LEVINSON, and RICHARD PETERSEN, An investigation into the status of <i>Iris thompsonii</i> (Iridaceae) ..... | 113 |
| ZEDLER, JOY B. (see FINK, BRIAN H.)   |     |
| ZUCCARELLO, GIUSEPPE (see WEST, JOHN A., and GIUSEPPE ZUCCARELLO)   |     |



# MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

## Contents

|  |        |
|--|--------|
| GENETIC UNIFORMITY OF EL ARBOL DEL TULE (THE TULE TREE)<br><i>Gustav W. Hall, George M. Diggs, Jr., Douglas E. Soltis, and Pamela S. Soltis</i>  | 1      |
| WILLIAM A. CANNON: THE SONORAN DESERT'S FIRST RESIDENT ECOLOGIST<br><i>Janice E. Bowers</i>  | 6      |
| TRICHOME PATTERNS AND GEOGRAPHIC VARIATION IN <i>LEPTODACTYLON CALIFORNICUM</i><br>(POLEMONIACEAE)<br><i>Patricia J. Gordon-Reedy</i>  | 28     |
| A SYSTEMATIC AND BIOGEOGRAPHIC REVIEW OF <i>RAILLARDIOPSIS</i> [ <i>RAILLARDELLA</i> ] <i>MUIRII</i><br>(ASTERACEAE: MADIINAE), WITH SPECIAL REFERENCE TO A DISJUNCT CALIFORNIA<br>COAST RANGE POPULATION<br><i>Bruce G. Baldwin and Donald W. Kyhos</i> | 43     |
| <i>ACCINELLIA HOWELLII</i> (POACEAE), A NEW SPECIES FROM CALIFORNIA<br><i>Jerrold I Davis</i>  | 55     |
| NOTES  |        |
| CHROMOSOME COUNTS IN <i>ASTRAGALUS</i> (FABACEAE)<br><i>Aaron Liston</i>   | 59     |
| NOTEWORTHY COLLECTIONS   |        |
| ARIZONA  | 60     |
| CALIFORNIA   | 62     |
| UTAH   | 62     |
| ANNOUNCEMENTS  | 62     |
| NEW PUBLICATIONS   | 42, 65 |
| SOUTHWESTERN BOTANICAL SYSTEMATICS SYMPOSIUM   | 54     |
| XV INTERNATIONAL BOTANICAL CONGRESS TOKYO  | 68     |



MADROÑO (ISSN 0024-9637) is published quarterly by the California Botanical Society, Inc., and is issued from the office of the Society, Herbarium, Life Sciences Building, University of California, Berkeley, CA 94720. Subscription rate: \$30 per calendar year. Subscription information on inside back cover. Established 1916. Second-class postage paid at Berkeley, CA, and additional mailing offices. Return requested. POSTMASTER: Send address changes to James R. Shevock, Botany Dept., California Academy of Sciences, San Francisco, CA 94118.

*Editor*—DAVID J. KEIL  
Biological Sciences Department  
California Polytechnic State University  
San Luis Obispo, CA 93407

*Board of Editors*

Class of:

- 1989—FRANK VASEK, University of California, Riverside, CA  
BARBARA ERTTER, University of California, Berkeley, CA  
1990—STEVEN TIMBROOK, Ganna Walska Lotusland Foundation, Montecito, CA  
THOMAS R. VAN DEVENDER, Arizona-Sonora Desert Museum, Tucson, AZ  
1991—JAMES HENRICKSON, California State University, Los Angeles, CA  
WAYNE R. FERREN, JR., University of California, Santa Barbara, CA  
1992—BRUCE A. STEIN, The Nature Conservancy, Washington, D.C.  
WILLIAM L. HALVORSON, Channel Islands National Park, Ventura, CA  
1993—JON E. KEELEY, Occidental College, Los Angeles, CA  
RHONDA L. RIGGINS, California Polytechnic State University, San Luis Obispo, CA

---

CALIFORNIA BOTANICAL SOCIETY, INC.

OFFICERS FOR 1989-90

- President:* ROBERT W. PATTERSON, Biological Sciences Department, San Francisco State University, San Francisco, CA 94132  
*First Vice President:* NIAL F. MCCARTEN, Department of Integrative Biology, University of California, Berkeley, CA 94720  
*Second Vice President:* MARY L. BOWERMAN, 970 Second Street, Lafayette, CA 94549  
*Recording Secretary:* RODNEY G. MYATT, Department of Biological Sciences, San Jose State University, San Jose, CA 95192  
*Corresponding Secretary:* BARBARA ERTTER, University Herbarium, University of California, Berkeley, CA 94720  
*Treasurer:* MONA BOURELL, Department of Botany, California Academy of Science, San Francisco, CA 94118  
*Financial Officer:* BARRETT ANDERSON, Department of Botany, California Academy of Science, San Francisco, CA 94118

The Council of the California Botanical Society consists of the officers listed above plus the immediate *Past President*, JOHN STROTHER, University Herbarium, University of California, Berkeley, CA 94720; the *Editor* of MADROÑO; three elected *Council Members*: JAMES SHEVOCK, Department of Botany, California Academy of Science, San Francisco, CA 94118; ELIZABETH MCCLINTOCK, University Herbarium, University of California, Berkeley, CA 94720; BRUCE PAVLIK, Department of Biology, Mills College, Oakland, CA 94613; and a *Graduate Student Representative*, JAMES D. MOREFIELD, Rancho Santa Ana Botanic Garden, Claremont, CA 91711.

|   |
|---|
| THIS PUBLICATION IS PRINTED ON ACID-FREE PAPER. |
|---|



# GENETIC UNIFORMITY OF EL ARBOL DEL TULE (THE TULE TREE)

GUSTAV W. HALL

Department of Biology, College of William and Mary,  
Williamsburg, VA 23185

GEORGE M. DIGGS, JR.

Department of Biology, Austin College, Sherman, TX 75090

DOUGLAS E. SOLTIS and PAMELA S. SOLTIS

Department of Botany, Washington State University,  
Pullman, WA 99164-4230

## ABSTRACT

An electrophoretic analysis of enzymes was conducted on leaf material from each of eight major segments of the Tule Tree, a huge specimen of *Taxodium mucronatum* from Oaxaca, Mexico, variously interpreted as a single enormous tree, or as a natural grafting of several individuals. For comparison, two nearby conspecific individuals were also analyzed electrophoretically. The results are consistent with the hypothesis that the Tule Tree is one genetic individual. The literature on the Tule Tree is reviewed.

## RESUMEN

Se llevó a cabo un estudio electroforético de enzimas en las hojas de cada uno de los ocho segmentos primarios del Arbol del Tule, un espécimen inmenso de *Taxodium mucronatum*, diversamente interpretado ya como un solo árbol enorme, o como producto de la fusión natural de varios árboles individuales. Para fines de comparación, dos ejemplares de la misma especie que crecían cerca, también fueron analizados por electroforesis. Los resultados obtenidos van de acuerdo con la hipótesis de que el Arbol del Tule es genéticamente un solo individuo. El artículo incluye una revisión de la literatura sobre esta extraordinaria planta.

El Arbol del Tule, a Montezuma Bald-cypress or Ahuehuete (*Taxodium mucronatum* Ten. [Taxodiaceae]) growing in a churchyard at Santa María del Tule, Oaxaca, Mexico, is often cited as the largest individual tree in circumference in the world (Goetz et al. 1985; Johnston et al. 1988; Russell et al. 1987). The Guinness Book of World Records (Russell et al. 1987) gives its height as 135 ft (41.18 m) with a girth of 117.6 ft (35.84 m) five feet above the ground. According to the Encyclopaedia Britannica (Goetz et al. 1985), basal circumference is 150 ft (45.75 m), if the bays and promontories of the buttressed trunk are followed. More than 20 men are reported necessary to encircle the trunk with outstretched arms (Johnston et al. 1988).

This tree, also known as El Gigante, has long been famous. Ac-



According to legend, this and two other large specimens were planted by a quetzalcoatl or prophet named Pecocho in the 6th century (Conzatti 1934). According to Martínez (1963), the first written reference to the tree is apparently that of Acosta (1590) who mentions a tree of enormous size three leagues from Oaxaca in New Spain. Cortes (Hora *in* Bateman et al. 1981) and Humboldt (Berry 1923; Lane 1953; Reyes 1884) or Bonpland (Reyes 1884) are reported to have seen the Tule Tree, with Lane (1953) stating that "Humboldt attached a plate to its massive trunk some 12 feet from the ground, whose inscription though partially overgrown by bark is still legible." Berry (1923) likewise cites Humboldt as having affixed a plate. Conzatti (1921) however, after an extensive search of the historical records, disputed such claims indicating there is no record of Cortes, Humboldt or Bonpland having seen the Tule Tree. Humboldt at least knew of the tree and discussed it in his Political Essay on the Kingdom of New Spain (1811) saying: "At the village of Santa María del Tule, three leagues east from the capital [Oaxaca], between Santa Lucia and Tlacochoyaya, there is an enormous trunc of cupressus disticha (sabino) of 36 metres in circumference. This ancient tree is consequently larger than the cypress of Atlixco, of which we have already spoken, the *dragonnier* of the Canary Islands, and all the boababs [baobabs] (*Adansonia*) of Africa."

The age of the Tule Tree is also controversial, at least in part due to the question of whether the tree is composed of one or several genetic individuals. Menninger (1967) cited age estimates of 2000–4000 years, whereas Berry (1923) gave 4000–6000 years. Conzatti (1934) quotes the Enciclopedia Universal Europeo-Americana as follows: "Humboldt, who estimated their [trees at Santa María del Tule] age at four thousand years, says that they are larger than the biggest baobabs to be found in Africa. De Candolle supposes their age to be six thousand years." Lane (1952) likewise reported that "Humboldt guessed that its [Tule Tree] age might be anywhere between 4000 and 6000 years." However, Conzatti (1934), despite an extensive literature search, was unable to find any mention of the age of the tree in the writings of either Humboldt or De Candolle.

At the other extreme of age estimates, Bowers (1965) cites H. A. Dutton, who reportedly examined the tree repeatedly, as rating the tree as a multiple-trunk growth, probably about 500 years old. This low age estimate conflicts with the report by Acosta in 1590 of a tree of enormous size three leagues from Oaxaca. Little *in* Enciclopedia Americana 1987, while noting that some experts believe el Arbol del Tule to be the world's oldest tree with an age of 4000 years, states that others would give estimates as low as 1000 years if it developed from more than one individual.

Possibly the most reasonable age estimate is that of Conzatti (1934) who believed the tree to be not more than 2000 years old. He makes



this estimate based on the very rapid growth of individuals of the species, comparative growth of other conifers and particularly on a comparison of the growth rate of branches from a nearby conspecific individual. While indicating that his figures are given only as an indication, with extrapolation he arrived at a likely age of approximately 1500 years.

The highly irregular outline of the trunk has given rise to speculation that this massive specimen may represent a natural grafting together of several individuals (Anza *in* Humboldt 1811; Bandelier *in* Alvarez 1900; Conzatti 1934; Dutton *in* Bowers 1965; Hora *in* Bateman et al. 1981; Little *in* Encyclopedia Americana 1987), perhaps similar individually to the adjacent large cypresses known as "hijos del Tule" or "el hijo y el nieto" (Martínez 1963). Others however, believe that only one individual is represented (Bolaños 1857; Charnay *in* Alvarez 1900; Ramírez *in* Alvarez 1900; Reyes 1884). Confusion over the individuality of the tree has led to problems concerning age estimates and to questions over the status of the Tule Tree as the world's largest in circumference. Enzyme electrophoresis can potentially clarify the origin of this renowned specimen.

#### MATERIALS AND METHODS

*Plant material.* Leaf samples were obtained from each of eight major segments (approximate compass directions: 0, 20, 70, 100, 160, 200, 220, 280 degrees) of the Tule Tree located at Santa María del Tule, approximately 9 km E of Oaxaca, Oaxaca, Mexico (Diggs and Diggs 4065). Leaf samples were also obtained from two other nearby large individuals ("hijos del Tule"). Vouchers have been deposited at BRIT and WS.

*Electrophoresis.* Leaf portions for electrophoresis were placed in plastic bags with wet paper towels and shipped to the laboratory. Electrophoretic procedures generally followed Soltis et al. (1983). Samples were prepared using the tris-HCl grinding buffer of Soltis et al. (1983) with 10% (wt/vol) PVP. Starch gel concentration was 12.5%.

The following enzymes were resolved: isocitrate dehydrogenase (IDH), leucine aminopeptidase (LAP), malate dehydrogenase (MDH), phosphoglucosomerase (PGI), phosphoglucosomutase (PGM), 6-phosphoglucosomate dehydrogenase (6PGD), shikimate dehydrogenase (SkDH) and triosephosphate isomerase (TPI). LAP, PGI, and TPI were resolved on a modification of gel and electrode buffer system 8 of Soltis et al. (1983) as described by Soltis and Soltis (1987). IDH, MDH, PGM, 6PGD and SkDH were resolved using system 9 of Soltis et al. (1983). Staining for all enzymes followed



Soltis et al. (1983) except LAP; staining for LAP followed Soltis and Soltis (1987).

## RESULTS AND DISCUSSION

Enzyme electrophoresis resulted in clear staining for eight enzymes encoded by 16 putative loci: *Idh*, *Lap*, *Mdh-1*, *Mdh-2*, *Mdh-3*, *Mdh-4*, *Mdh-5*, *Pgi-1*, *Pgi-2*, *Pgm-1*, *Pgm-2*, *Skdh-1*, *Skdh-2*, *6pgd*, *Tpi-1*, and *Tpi-2*. The observed bands migrated anodally for all enzymes examined.

The number of isozymes observed for the enzymes examined is consistent in most instances with reports for other seed plants (Gilchrist and Kosuge 1980; Weeden and Gottlieb 1980; Gottlieb 1981, 1982). However, for 6PGD only one isozyme was observed, whereas two isozymes would be expected in diploid seed plants (Gottlieb 1981, 1982). The presence of only one isozyme when two are expected could be due to: 1) comigration of the two isozymes, or 2) the loss of expression of one isozyme, perhaps as a result of the length of time involved in transporting the material from the field to the laboratory. In support of the latter hypothesis is the observation that one of the two observed isozymes was only faintly stained for PGI, PGM, and TPI.

*Idh*, *Lap*, *Mdh-1*, *Mdh-2*, *Mdh-3*, *Mdh-4*, *Mdh-5*, *Pgi-1*, *Pgi-2*, *Pgm-1*, *Pgm-2*, *Skdh-1*, *6pgd*, *Tpi-1*, and *Tpi-2* were monomorphic, with all samples of the Tule Tree, as well as the two neighboring trees sampled, displaying bands of identical electrophoretic mobility. The findings for these monomorphic loci are in agreement with the idea that the Tule Tree is a single individual, but are equivocal given that the neighboring trees displayed the same allozymes. Significantly, all samples of the Tule Tree were heterozygous for *Skdh-2*, exhibiting *Skdh-2ab*. In contrast, both neighboring trees possessed only *Skdh-2b*. The fact that all eight samples of the Tule Tree were heterozygous for *Skdh-2*, whereas both neighboring trees were homozygous, provides the strongest evidence in support of the hypothesis that the Tule Tree originated from only a single seedling.

## CONCLUSIONS

More data on the amount of genetic variation to be expected in the species and on the occurrence of natural grafting would enhance a judgment as to the origin of this tree. However the genetic data are in agreement with the hypothesis that only one genetic individual is involved. Most noteworthy is the fact that all samples from the Tule Tree displayed the same heterozygous phenotype for *Skdh-2*, in contrast to the homozygosity of the nearby trees. Our results further strengthen the traditional interpretation of El Arbol del Tule as a truly exceptional individual.



## ACKNOWLEDGMENTS

We thank John West for assistance with interlibrary loan material and Maria Cecilia Salisbury for translation of the abstract.

## LITERATURE CITED

- ACOSTA DE, P. J. 1590. Historia natural y moral de las Indias. Casa de Juan de Leon, Seville. 1894 Reprinted Edition, Ramón Anglés, Madrid.
- ALVAREZ, M. F. 1900. Las ruinas de Mitla y la arquitectura. Talleres de la Escuela N. de Artes y Oficios para Hombres, Mexico.
- BATEMAN, G. et al. (eds.). 1981. The Oxford encyclopedia of trees of the world. Oxford University Press, Oxford.
- BERRY, E. W. 1923. Tree ancestors. Williams and Wilkins Co., Baltimore.
- BOLAÑOS, J. N. 1857. El árbol de Santa María del Tule. Bol. Soc. Mex. Geogr. Estad. 5:363. [Reprinted in Alvarez 1900.]
- BOWERS, N. A. 1965. Cone bearing trees of the Pacific coast (7th printing). Pacific Books, Palo Alto, CA.
- CONZATTI, C. 1934. Monograph on the tree of Santa María del Tule. (Translated from the 1921 original Spanish edition by Ralph Summers.) Imprenta Mundial, Mexico.
- ENCYCLOPEDIA AMERICANA. 1987. The encyclopedia Americana (international edition). Croler Inc., Danbury, CT.
- GILCHRIST, D. G., and T. KOSUGE. 1980. Aromatic amino acid biosynthesis and its regulation. Pp. 507–529 in B. F. Mifflin (ed.), The biochemistry of plants, Vol. 5. Academic Press, New York.
- GOETZ, P. W. et al. (eds.). 1985. The new encyclopaedia Britannica, 15th ed., vols. 11, 28. Encyclopaedia Britannica, Inc., Chicago.
- GOTTLIEB, L. D. 1981. Electrophoretic evidence and plant populations. Prog. Phytochem. 7:1–46.
- . 1982. Conservation and duplication of isozymes in plants. Science 216: 373–380.
- HUMBOLDT, F. H. A. 1811. Political essay on the kingdom of New Spain. (Translated from the original French by John Black.) Longman, Hurst, Rees, Orme, and Brown, London.
- JOHNSTON, B. et al. (eds.). 1988. Collier's encyclopedia. Macmillan Educational Co., New York.
- LANE, F. C. 1953. The story of trees. Doubleday and Company, Inc., Garden City, NY.
- MARTÍNEZ, M. 1963. Las Pináceas Mexicanas, 3rd ed. Universidad Nacional Autónoma de México, México.
- MENNINGER, E. A. 1967. Fantastic trees. The Viking Press, New York.
- REYES, O. 1884. El sabino de Santa María del Tule. La Naturaleza (Mexico City) 6:110–114.
- RUSSELL, A. et al. (eds.). 1987. Guinness book of world records. Sterling Publishing Co., Inc., New York.
- SOLTIS, D. E., C. H. HAUFLER, D. C. DARROW, and G. J. GASTONY. 1983. Starch gel electrophoresis of ferns: a compilation of grinding buffers, gel and electrode buffers, and staining schedules. Amer. Fern J. 73:9–27.
- and P. S. SOLTIS. 1987. Breeding system of the fern *Dryopteris expansa*: evidence for mixed-mating. Amer. J. Bot. 74:504–509.
- WEEDEN, N. F. and L. D. GOTTLIEB. 1980. The genetics of chloroplast enzymes. J. Hered. 71:392–396.

(Received 6 Jun 1989; revision accepted 10 Oct 1989.)



WILLIAM A. CANNON  
THE SONORAN DESERT'S FIRST RESIDENT ECOLOGIST

JANICE E. BOWERS  
U.S. Geological Survey, 300 West Congress, FB-44,  
Tucson, AZ 85701-1393

ABSTRACT

William Austin Cannon (1870–1958) was the first resident investigator at the Carnegie Institution of Washington's new Desert Laboratory in Tucson, AZ. He pioneered in the physiological ecology of desert plants and in the study of root systems, particularly the effects of oxygen and temperature on root growth. He also held a worldwide interest in desert ecosystems. Well-known during his lifetime, he has since been largely forgotten.

“Dr. W. A. Cannon has been selected as resident investigator of the Desert Botanical Laboratory of the Carnegie Institution,” read the anonymous notice in the *Botanical Gazette* for February 1903.<sup>1</sup> Six months later, Cannon (Fig. 1) arrived in Tucson, then a small desert town of 7500. The recently erected laboratory building stood halfway up Tumamoc Hill two miles west of downtown Tucson. The laboratory grounds included more than 800 acres of surrounding desert.

This unique establishment owed its existence to the farsightedness of Frederick V. Coville, curator of the U.S. National Herbarium, who, during his exploration of Death Valley in 1891, had been impressed by the adaptations of desert plants to their harsh environment. Clearly, the desert was a unique and little-known ecosystem; equally clearly, what was needed was a research station devoted to desert investigations. When he presented this idea to the botanical advisory committee of the Carnegie Institution of Washington, they not only concurred, they provided \$8000 to construct a building, furnish laboratory equipment and pay the salary of a resident investigator for one year.<sup>2</sup> Coville and Daniel T. MacDougal, director of laboratories at the New York Botanical Garden, then toured the Southwest to find the most suitable site and selected Tucson because, among other advantages, it was accessible by rail and located in undisturbed desert.

Both Coville and MacDougal were already well-established scientists and doubtless neither cared to assume the post of resident investigator for a yearly salary of about \$2000 plus \$25 a month for out-of-pocket expenses. They selected William Cannon, and by 1 September 1903, he was on the spot, the Sonoran Desert's first resident ecologist.





FIG. 1. William A. Cannon (1906). Courtesy of Arizona Historical Society.

Cannon, then thirty-three, had been MacDougal's assistant at the New York Botanical Garden, where he investigated the anatomy of plant hybrids (Cannon 1902a, 1903a, b, 1904a). A late bloomer, he had earned his bachelor's degree at twenty-eight, his doctorate at Columbia University at thirty-one. While working towards a master's degree at Stanford University, he had considered such divergent botanical subjects as redwoods and giant kelp, turning his mind to the plant geography of one and the evolutionary ecology of the other (Cannon 1901a, b). He was already accustomed to thinking like an ecologist, then, when MacDougal offered him the job of resident investigator.

The new Desert Laboratory was devoted to ecology before the very word was widely used. Like most of his ecological contemporaries—Henry Gleason, Frederic Clements, Henry Cowles, Frederick Coville, Edgar Transeau, Forrest Shreve—Cannon had a foot in two worlds: traditional botany, especially anatomy and morphology, and the budding field of plant ecology.<sup>3</sup> His interest in plant ecology thrived at the Desert Laboratory, and in 1915 he became one of 268 charter members of the Ecological Society of America, along with Shreve and MacDougal (Burgess 1977).

Cannon started work with instructions to inquire into the "morphology, physiology, habit, and general life-history of the species indigenous to the deserts of North America" (MacDougal 1903, p.



249). As he settled in, he could envision enough research ahead to keep him busy a long time, and he was, he told MacDougal, very much pleased with the prospect.<sup>4</sup>

First, however, he had to supervise completion of the laboratory. The interior still lacked woodwork, floors, and wiring. The gasoline-powered pump for the water system needed to be inspected and the new road up Tumamoc Hill required substantial improvement. Bills had to be settled, equipment installed, botanical textbooks and manuals purchased, and the corners of the property located. Also, installation of a telephone was mired in local politics. Finally, after two months of nagging contractors and tying up loose ends, Cannon was able to notify MacDougal that "the contractors should be out of this building and we in before the end of the week."<sup>5</sup>

Ready to begin research at last, he selected *Fouquieria splendens* as his first subject because "it responds so delicately to its surroundings." Someone had told him that "a very little encouragement in the way of rain in the summer is sufficient to make it send out . . . leaves . . . in a surprisingly short time."<sup>6</sup> He planned to study its anatomy first, then its root system and physiology. Soon, under prodding from MacDougal, he agreed to study "some fleshy form," too, and selected *Ferocactus wislizenii*.

Cutting cross-sections of *Fouquieria* stems for anatomical study proved surprisingly difficult, but Cannon substituted ingenuity for the more usual microtome. By softening the tissues in glycerine first, then sawing at the stems with two different razor blades, he managed to obtain adequate material. Before the year was out, he also studied *Ferocactus* anatomy, measured transpiration of *Mammillaria microcarpa*, determined the water content of a full-grown *Ferocactus*, and measured diameter changes in *Ferocactus* and *Carnegiea gigantea*. He was, apparently, the first scientist to suggest that columnar cacti "must undergo considerable seasonal and daily change in diameter owing chiefly to alterations in temperature and water supply, and that if they did, the corrugations would come in very neatly in permitting the adaptations to these variations."<sup>7</sup>

Meanwhile, Volney M. Spalding, an elderly botany professor from the University of Michigan, had become the Desert Laboratory's first visiting investigator. When he arrived in December 1903, he found Cannon devising a novel method for measuring transpiration according to some suggestions MacDougal had made. Cannon helped the older gentleman settle in and told MacDougal, "He is a continual inspiration[,] . . . a good one to set the ball rolling."<sup>8</sup> The innumerable opportunities for research must have seemed overwhelming at first, and Cannon welcomed Spalding's steadying influence and botanical knowledge. With assistance and advice from Spalding, then, Cannon continued to refine his transpiration-measuring apparatus.

Physiologists then measured transpiration by three different meth-



ods, none of which could be used on living plants in situ. Cannon ingeniously skirted this difficulty by devising a portable apparatus. His method had the further advantage of being noninjurious, therefore suitable for repeated measurements on the same plant over days or weeks (Cannon 1905a). Basically, he created an airtight compartment by pouring a cement slab under a plant and setting a bell jar over both plant and slab. Before sealing the jar in place, he put a hygrometer and a thermometer inside. The change in absolute humidity over a period of time, calculated from relative humidity and temperature, equaled the amount of vapor transpired by the plant (Cannon 1905a).

In spite of certain drawbacks, this method worked well enough that in one year he measured the transpiration of *Carnegiea*, *Larrea tridentata*, *Encelia farinosa*, and *Fouquieria*, collecting the first data on transpiration in desert plants. In fact, his investigation of *Fouquieria* transpiration (Cannon 1905b) was among the earliest physiological studies of North American xerophytes. (The first, Spalding's 1904 study of *Larrea*, relied partly on transpiration data that Cannon had gathered.)

Although transpiration work must have filled much of 1904 (by May he had made more than seventy-five measurements), he also studied *Phoradendron* germination with special emphasis on how seeds penetrate their host (Cannon 1904b); visited the San Francisco Peaks in northern Arizona (Cannon 1906a); and excavated root systems of *Ferocactus*, *Larrea*, *Carnegiea*, and other desert plants.

As Cannon studied the adjustment of plants to their desert environment, he himself adjusted to his still unfamiliar surroundings. An unseasonably heavy rainfall in May stimulated new leaves on *Fouquieria* and *Larrea*, and he told MacDougal that he was "looking for a spring growth of annuals but thus far none have appeared."<sup>9</sup> None *did* appear, of course, until the following February, when good winter rains made the desert "a veritable paradise."<sup>10</sup> When he first arrived, the weather had been unusually cool for September, and he was quite willing to "wait another year before experiencing the hottest weather Tucson can put up."<sup>11</sup> When this came to pass the following June, he said that "even the most hardened liar among the natives will hardly defend this summer climate."<sup>12</sup> The weather held yet more surprises. In mid-August, when he returned from his trip to the San Francisco Peaks, he found "quite another country from the desert that we had left a little over two weeks before"<sup>13</sup> as lifeless shrubs burst into leaf and flower in response to summer rains.

With the summer came visiting investigators whose academic calendars freed them for three months of research. They included Francis Lloyd, a plant anatomist from Columbia University, and Burton Livingston, a plant physiologist associated with the University of Chicago. Cannon helped them settle in and rounded up suit-



able apparatus for their experiments. Another visitor that summer was Coville, whose surprise visit satisfied him that everything was “in first rate shape, including enthusiasm and progress.”<sup>14</sup> Cannon welcomed the influx of visitors. There was no lack of research problems to keep them all busy; as he told MacDougal, their main difficulty was “to choose wisely from the abundance.”<sup>15</sup>

As resident investigator, Cannon bore the particular responsibility of justifying the Carnegie Institution's initial investment. The Desert Laboratory had been founded on a provisional basis, and its funding was appropriated year by year. If, after its first five years, it showed sufficient promise, it was to become a permanent research station (Bowers 1990). Before the lab was a year old, Coville let Cannon know that “we are looking for a fine large paper from you. The future of the laboratory will be much influenced by the character of this paper and by the discoveries it contains.”<sup>16</sup>

The future arrived two years before the end of the probationary period. After Institution president Robert Woodward visited in July 1905, he proposed to greatly enlarge the scope of the laboratory by increasing the work force, constructing staff residences, and remodeling the building. Best of all, he wanted to make the Desert Laboratory a permanent station as soon as possible. This was, as MacDougal told Cannon, “immensely gratifying. . . . it is very pleasing indeed to know that the things you are doing are being appreciated in this way.”<sup>17</sup>

MacDougal was appointed director of the Desert Laboratory effective 1 January 1906, and immediately began to enlarge his staff. Cannon was kept on, and, to his delight, Spalding, Lloyd, and Livingston were added to the roster of staff scientists. “They all have had considerable experience here and will come with good conceptions of the extent as well as the nature of the work to be undertaken,” he told MacDougal.<sup>18</sup>

Shortly thereafter, Cannon published a popular article about the Desert Laboratory (Cannon 1906c), a kind of manifesto for the nascent field of plant ecology. Desert Laboratory scientists, Cannon noted, “reach out in two directions: they endeavor to record as fully as possible the environmental factors which surround and which influence every day the plants of the desert, and they endeavor to note and to measure as fully and as accurately as possible the reactions of these plants to these stimuli” (Cannon 1906, pp. 30–31). He listed problems that confront the desert biologist: how do desert conditions differ from those in humid areas? how do endemic plants react to these conditions? where did desert plants come from? how and when did they become adapted to the desert?

With the continuity of the Desert Laboratory assured, the staff initiated an extraordinary range of research projects (Bowers 1990). Spalding set up nineteen permanent plots on the Desert Laboratory



grounds and mapped the vegetation of each. MacDougal monitored plant succession at the recently formed Salton Sea and undertook a series of experiments aimed at elucidating the mechanisms of inheritance. Forrest Shreve, who joined the staff in 1908, examined establishment of desert perennials and frost tolerance of *Carnegiea*. Livingston continued his work on evaporation and transpiration. Plant physiologist Herman Spoehr concentrated on photosynthesis. Lloyd continued his anatomical studies.

Several years earlier, the president of the Carnegie Institution had worried that Desert Laboratory researchers, working in close proximity on similar problems, would infringe on one another's scientific territory. He had even asked if Cannon had any objection to assisting summer investigators, since "they might possibly take undue advantage of the knowledge they may gain from you and anticipate you in the publication of important results."<sup>19</sup> Cannon had promptly replied that "the ground for work here is so broad that several botanists could work at one time not only without 'jumping' each other's claim but to their great mutual advantage."<sup>20</sup>

True as this was then, Woodward's forbodings acquired substance before too long. There is, as Paul B. Sears noted in another context, an ecology of ecologists (Sears 1956). Just as coexisting animal species create unique niches by partitioning available resources, so coexisting ecologists partition the field of research. At first, as Cannon had indicated, the need for partitioning hardly existed. As more researchers arrived, however, division of research opportunities inevitably (and probably unconsciously) took place. With Livingston concentrating on transpiration and the physical environment, Lloyd on anatomy, Spalding (and later Shreve) on vegetation and plant geography, and MacDougal on anything that took his fancy, Cannon had little choice but to narrow his field of research. Although he continued his anatomical and ecological studies for a few more years—between 1906 and 1908, he examined the distribution of chlorophyll in nineteen species of desert plants (Cannon 1908a), measured salt concentration in the sap of halophytes (Cannon 1908b), and studied inheritance in plant hybrids (Cannon 1908c, 1909a)—after 1908 he specialized in roots.

Begun as one among many lines of research, these root investigations proved "wonderfully enticing,"<sup>21</sup> and between 1909 and 1954 he published some two dozen papers on the subject. In 1909, the study of root systems was virtually untouched,<sup>22</sup> as Cannon noted: "The character and extent of the root systems of desert plants, as well as the role which they play in the distribution of these plants, are in the main not known." He recommended investigating roots in relation to soil moisture, temperature, oxygen, and adjacent plants. "The influence of these and other factors on the presence of plants in their peculiar habitats are among the most pressing problems of



desert botany that await studious inquiry," he wrote (Cannon 1909b, p. 59). With these words he mapped out enough research to fill the next forty-five years.

He quickly made several novel discoveries: that the roots of seedling *Opuntia versicolor* act as water storage organs (Carnegie Yearbook 1906); that *Orthocarpus purpurascens* was a root parasite on at least eighteen different hosts (Cannon 1909c); that *Krameria grayi* was also parasitic (Cannon 1910a); and that certain desert shrubs produce ephemeral rootlets to take maximum advantage of brief rainy periods (Cannon 1912a). He posited that the shallow roots characteristic of cacti went hand in hand with their succulence; since the upper soil layers dry out quickly, "plants depending on this stratum for moisture must either be short-lived or have the capacity of storing up water against the period of drought" (Cannon 1913, p. 420; see also Cannon 1909b).

In 1911 he summarized his first five years of root research in the classic *Root Habits of Desert Plants*. His ultimate goal, he wrote, was to conduct root studies on "broad physiological-ecological grounds," which to him meant primarily experimental work. First, however, he required exact descriptions of root systems, therefore he undertook "the prosaic work of excavating" (Cannon 1911, p. 10). He dug up annuals with roots intact; perennials he studied in place, first removing the soil, then fixing a grid of measuring tapes above the exposed roots and drawing them to scale.<sup>23</sup> After examining the roots of twenty-one desert perennials and thirty-six summer and winter annuals, Cannon stated conclusively that, contrary to the widespread belief that the roots of desert plants were uniformly deep, they were instead "extremely variable as regards depth of penetration, lateral extent, and other characteristics, and . . . no one type of root can be said to be the prevalent one" (Cannon 1911, p. 8). He grouped desert root systems into one generalized and two specialized types. Plants with generalized root systems showed good development of both tap and lateral roots, he said. Most desert perennials belonged to this category. Specialized root systems featured either deep tap roots or shallow laterals. The heteromorphic root systems typical of cacti possessed both an anchoring portion and an absorbing one (Carnegie Yearbook 1910).<sup>24</sup>

Although most interested in root physiology, Cannon did discover many interesting ecological relationships as he excavated. When he found that the root system of one *Larrea* was penetrated by roots from sixty others, he commented that "competition between neighboring *Covillea* [*Larrea*] on the bajada, for soil water, is presumably keen" (Cannon 1911, p. 61). If near neighbors belonged to different species, however, no direct competition for water ensued, since their roots occupied horizontal layers at different depths (Carnegie Yearbook 1909).<sup>25</sup> His ideas about competition contradicted those of



Shreve, who categorically denied the existence of competition in desert plant communities (Shreve 1911, 1915, 1917, 1936).<sup>26</sup>

Cannon deduced that “plants having roots which reach to greater depths than 15 cm. can obtain some moisture at all seasons,” whereas shallower roots could absorb water only after rains. Seedlings, in order to survive, “must send their roots below 15 cm. within six weeks following the close of a stormy period” (Cannon 1911, pp. 16–17).

He saw a close relationship between root type and plant distribution: plants with prominent tap roots required deep soil and would be limited in their distribution, while those with generalized roots could grow in a variety of habitats and would be broadly distributed. This was a point he reiterated many times (Cannon 1906b, 1911, 1913a, b, 1915a, 1925a); evidently he seldom thought to look for aboveground determinants of plant distribution.

Starting in 1907, Cannon spent part of each year on the California coast. This was the result of the Carnegie Institution’s support of plant breeder Luther Burbank, stationed in Santa Rosa, CA. Cannon, by virtue of his background in cytology, was asked to make cytological and histological examinations of Burbank’s hybrids (Cannon 1908c, 1909a). He set up temporary headquarters at the Hopkins Seaside Laboratory in Pacific Grove, but before the summer was over, officers of the Carmel Development Corporation offered to provide a permanent site—three acres of land and a new laboratory building in Carmel-by-the-Sea. MacDougal liked the idea immensely; a seaside laboratory would be a refreshing retreat from Tucson summers, and it would “give the administration the idea that we are being appreciated.”<sup>27</sup> The institution approved the plan in December 1908, and the following summer, the Coastal Laboratory was ready for occupancy.

At the new laboratory Cannon was at first relegated to the role of MacDougal’s research assistant, reporting on the growth and survival of transplants in the experimental garden. Eventually, as MacDougal spent more time at the Coastal Laboratory, Cannon was freed to undertake his own research once again and to make excursions to nearby points of botanical interest—the endemic groves of *Pinus radiata* on the Monterey peninsula, for example, or the populations of *Abies bracteata*, another endemic, in the Santa Lucia Mountains. These trips often combined his dual interests in plant ecology and root systems. After the chaparral understory was cleared from *P. radiata* groves, he noticed, the pines died within two years. He speculated that, once its protective cover was removed, the soil dried out during the long, rainless summers, and the pines died of drought (Cannon 1913d). He discovered that *Quercus agrifolia*, characterized by extensive feeder roots, was “wholly dependent upon the water coming directly from the rains or . . . run-off,” and “for



this reason, the roots of adjacent trees compete . . . in a manner exactly comparable to desert shrubs. Thus it follows that, because of a relative paucity of water, the trees come to have an open stand" (Cannon 1914b, p. 423). This was also true of *Q. douglasii* but not of the deeply rooted *Q. lobata*, a floodplain species.

Having launched the Coastal Laboratory, Cannon promptly left it for a trip to the Algerian Sahara. The reason for this journey is not entirely clear. Possibly MacDougal, who never lacked for big ideas, suggested it; he told one correspondent that Cannon was "having a most profitable time in extending some of our lines of work here into the Sahara." In fact, he added, he expected similar developments for many of their research projects.<sup>28</sup> Cannon's official reason for his Saharan trip was to "examine the more obvious features of the physiological conditions prevalent in the region . . . and, in connection with these observations, to make some detailed studies of the root-habits of the most striking species of the native flora" (Cannon 1913b, p. 1). For whatever reason, Cannon left for Algeria via London and Brussels in April 1910.

Arriving in Algiers in October, he traveled across the Atlas Mountains and into the Sahara, a round trip of 1000 miles by horse-drawn carriage, motorcycle, and camel. In February he traveled up the Nile to Aswan, then returned to Algeria, where he made Biskra his headquarters for a month of local excursions. In April he left for Europe, and by the middle of May he had written a substantial proportion of *Botanical Features of the Algerian Sahara* (Cannon 1913b).

During his Algerian sojourn, he excavated the roots of sixteen species and conducted seven "censuses" of vegetation in sixteen-meter-square plots.<sup>29</sup> Of more interest is the rich comparative material he gathered on desert environments. His knowledge of the Arizona desert gave him a unique perspective on the Algerian Sahara. Around Tucson, he said, warm-season rainfall promoted a rich succulent flora; farther west, where the rainy season was limited to the winter months, few succulents occurred. Similarly, in Algeria, where the single rainy season occurred during the winter, "the absence of plants with water-storage facilities" was a prominent feature of the vegetation (Cannon 1913b, p. 69).<sup>30</sup> In the extreme desert of the Algerian Sahara, plants struggled mainly with their environment and competition was negligible. Competition was readily apparent in regions that were not quite so arid, however, as in the vicinity of the Desert Laboratory.

He was startled by the enormous number of grazing animals in southern Algeria—nearly two million sheep, 588,000 goats, and 126,000 camels. Only the poisonous, distasteful, or well-armed plants escaped consumption, he noted. Again, his experience in Arizona, where plants were spicier than in Algeria but only lightly browsed, provided a fruitful comparison, and he concluded that the evolution of spiciness had little to do with browsing animals (Cannon 1913b).



After Cannon returned to Tucson in September 1911, he devoted himself to experimental studies. In 1912 and 1913 he tackled the vertical placement of root systems with reference to soil moisture and aeration, then, in 1914 and 1915, in relation to soil temperature (Cannon 1913a, c, 1915a, 1916, 1917a, 1918; Cannon and Free 1917). He devised his own equipment for some of these experiments: a simple root-growth box, for instance, and more elaborate "thermostats," glass tubes in which roots could be held at constant temperatures or charged with oxygen, helium, or other gases. Between 1916 and 1918 he investigated the joint effects of temperature and aeration on root growth, varying the gaseous elements introduced into root systems. "I have run through one set of mesquite seedlings on a nitrogen diet and they came off unscathed," he reported. "But the opuntia I am now watching seems to behave quite differently, growth slowing very markedly."<sup>31</sup> By this time, the Coastal Laboratory had undergone extensive remodeling, and working there was, Cannon reported, "more fun than a goat."<sup>32</sup>

These methodical experiments made several novel contributions. He learned that unrelated species in the same habitat could react differently to soil temperature, as did *Fouquieria* and *Prosopis velutina* (Cannon 1915a). Cannon and soil scientist Edward Free were the first to point out that response to soil oxygen was also species-specific and that species could vary widely in their oxygen requirements (Cannon and Free 1917). Cannon demonstrated that roots of cacti cannot extract water from cold soils, thus "in regions where cacti are abundant, either native or introduced, rains occur during the warm season" (Cannon 1916, p. 441; see also Cannon 1915a, 1925a). He defined a root-growth index, TR, that was "the summation of root growth at the temperatures employed" (Cannon 1918, p. 64); he noted that when a species is limited in distribution by unfavorable temperatures, TR should be small at the edge of its range and large in the center. He even suggested that TR could be plotted as isolines, thus showing the relation between root temperature and distribution.

These experiments emphasized artificial systems that examined a single parameter at a time. As one plant physiologist recently pointed out, such studies leave "a void in understanding the mechanisms regulating root development in natural environments" (Feldman 1988, p. 618). Cannon evidently never noticed this limitation in his work. He criticized Weaver's *Ecological Relations of Roots* (Weaver 1919) for failing to identify soil temperature and soil aeration as potential limiting factors in root development (Cannon 1920), yet he himself failed to consider myriad other aspects of root development such as genetic constraints, hormonal control, soil strength, geotropism, and root exudates.

"Cannon is still bent on going to Australia and asserts that he has discovered no conditions which would in any way impede his movements," MacDougal told a friend in July 1917.<sup>33</sup> Having already



cancelled a trip to southern Europe and Palestine, Cannon was evidently determined that U.S. involvement in the war would not interfere with his plans a second time, and he prevailed upon MacDougal to write a letter to the State Department assuring them that the proposed trip was "imperative." MacDougal obliged, and in April 1918 Cannon was on his way with the Carnegie Institution's permission to work at his own expense for one year while drawing his regular salary.

Within a month of his arrival in Sydney, he had surveyed the country around Oodnadatta, a "sure enough desert," and drawn up plans for fieldwork: "After working over the 'Mulga' zone, which should furnish much of interest, and of course after seeing this region, I will go west of Port Augusta into the 'Mallee' zone and study its characteristics. These two, with the desert, should make a good story."<sup>34</sup> By the middle of August he had collected some 100 herbarium specimens, taken "a splendid series of photographs of habitats and plant habits," and amassed a "considerable body of notes." If not for the war, he told MacDougal, he would request an extension of his leave because "problems and new points of view are opening up constantly."<sup>35</sup>

Cannon's experience in South Australia reinforced his earlier impression that season, timing, and amount of rainfall were paramount in determining the vegetation of arid regions. "So far as the well-being of the vegetation is concerned," he wrote, "the reliability of the rains . . . is of capital importance. And in a general way the reliability of the rains decreases with the decrease in the amount of rainfall, which it will be seen only serves to intensify the effects of progressive aridity" (Cannon 1921, p. 8). Using five years of rainfall data from six different stations, he estimated that the ecologically effective rainfall would be 0.15 inch or more and that the percentage of noneffective rainfall would rise as the yearly total precipitation decreased.<sup>36</sup>

As in Algeria, he examined root systems when the opportunity arose. He discovered that, in very dry regions, "the limit of root penetration may coincide with the depth of the penetration of the rains. . . . For this reason, in regions where the general penetration of the rains is slight, the placing of the roots of perennials is necessarily superficial" (Cannon 1921, p. 137). Weaver (1926) later corroborated this point.

While in Australia, Cannon largely set aside his experimental predilections and functioned more as ecologist than physiologist. He noted that the various trees and shrubs all bore a "xerophytic stamp," but despite their superficial monotony, they showed "a bewildering variety of adjustments" to their arid environment (Cannon 1921, p. 1). Perennials tended to develop markedly long leaves that, in the case of *Acacia*, were actually phyllodes. He hypothesized that the



length-to-width and area-to-length ratios of leaves and phyllodes could be used as an index of their xerophily. In mesophytic leaves in general, the ratio of area to length was 40:1, but among South Australia plants, it was roughly 5:1, an indication of how aridity had selected for leaves with smaller transpirational surfaces.<sup>37</sup> Phyllodes could be up to twenty-four times longer than wide, which again showed adaptation to the unfavorable water supply. Other water-saving features of leaves included hairs, resinous secretions, heavy cuticles, and sclerenchymous tissue.<sup>38</sup>

Cannon wrote the first draft of *Plant Habits and Habitats in the Arid Portions of South Australia* on the homeward journey while his experiences were still fresh in his mind. The book shows him to good advantage as a physiological ecologist whose interests were not bounded by laboratory walls. Field studies complement experimental work, he wrote, and although "it has not been practicable to carry out direct experiments on subjects suggested by the observations, it has been of interest and profit to interpret the observations so far as possible in the light of experimental results already accomplished" (Cannon 1921, p. 2).

When Cannon came home in May 1919, he resumed root experimentation at the Coastal Laboratory, now his research home. He also made plans for a year-long stay in South Africa, and, despite difficulties in obtaining funds from the Carnegie Institution, left for Pretoria in the spring of 1921. Through the courtesy of Pole Evans, a South African botanist, he was given a first-class rail pass, and the Botanical Survey of South Africa offered to pay the remainder of his traveling expenses. His itinerary allowed for brief stays in the Little Karroo, the High and Low veldts, and the Namib, and a prolonged sojourn in the Central Karroo.

Cannon embarked on this trip primed with his knowledge of arid regions on three continents. Each region presented its own problems which required specific study: "even the common fact of aridity is exceedingly complex, possibly with unlike causes and characteristics as well as with dissimilar physiological and ecological relations" (1924a, p. 7). The flora and vegetation of each region were also distinct, and even a single genus, *Acacia* for example, did not behave uniformly from one desert to another. He found it impossible to outline a set of traits that would distinguish between plants of arid and semiarid regions. Although certain features were common to virtually all arid-adapted plants (recessed stomates, trichomes, reduced leaves, double epidermis, heavy cuticles),<sup>39</sup> there was no morphological type that was completely "eremological," that is, limited to arid lands. (Oppenheimer confirmed this point: "If true xerophytes are not all xeromorphous, conversely xeromorphous plants are not all xerophytes" [Oppenheimer 1960, p. 106].)

Structural adaptations to aridity had long interested Cannon. As



early as 1908, he had noted that leaflessness and reduced leaves enable desert plants to lessen their transpiring surface. Certain species oriented their branches to protect leaves from intense midday illumination. Cannon had concluded that many xeromorphic characters could hardly “be attributed to the molding influence of the environment; it will doubtless be necessary to take into consideration the peculiar history of each plant, its gradual modification from its remote mesophytic ancestor, before habits and structure are satisfactorily related” (Cannon 1908a, p. 4).

Sixteen years later, after working in deserts around the world, he was ready to do just that—relate structure, evolution, and habitat. Two kinds of forces—heredity and the immediate environment—determined anatomical structure, he said (Cannon 1924a). Physiologists, often little accustomed to extremely arid regions, tended to stress environment in their studies of desert plants. He attempted to redress this imbalance by comparing the anatomy of arid-adapted plants with that of mesophytic relatives. Xerophytes had followed “very diverse morphological roads . . . during the long processes of adjustment” to aridity, he concluded (1924a, p. 110). Such xerophytic features as thick cell walls and well-developed sclerenchyma were “in part a modification of family structures by reason of which . . . survival is accomplished” (1924a, p. 120).

His comparative studies of arid regions led him to point out convergent evolution (although he did not use this term) in desert plants. Although, he wrote, desert perennials in general showed a marked diversity in growth-form, “species belonging to different genera, and even of different families, may be strikingly alike, although superficially so” (1924a, p. 155). Examples included the African genus *Aloe* and the American one *Agave*, and certain African species of *Euphorbia* and American *Echinocereus*. In the course of evolution, he explained, “species react to . . . common impinging environmental factors. Where reactions take fairly parallel courses, the results are to a certain degree harmonious, and to the degree that they are so the species tend to become more and more alike” (1924a, p. 158).

Cannon described *General and Physiological Features of the Vegetation of the More Arid Portions of Southern Africa* as the third of a series in his “minor research.” The series itself, occasional papers on the botanical features of arid regions, was eventually to culminate in “a physiological–ecological work of a comprehensive nature on deserts in general” (1924a, p. 7). This ambitious work never came to pass; upon his return from South Africa, Cannon immersed himself once again in experimental studies of roots.

These root investigations, too, were to be initial steps in a more ambitious program: according to Cannon, “the ultimate aim of the



investigations is to acquire data which will define as clearly as may be practicable the role played by the root in the activities of the plant as a whole" (Carnegie Yearbook 1922–1923, pp. 56–57). In *Physiological Features of Roots*, a monograph that summarized his numerous experiments, he presented a more detailed outline of his research goals. "Investigations should be carried out on the mutual relation of root and of shoot, particularly with reference to the effect on root-growth," he wrote (Cannon 1925a, p. 11). He recommended investigations of respiration in healthy and diseased roots, of gas exchange in roots, of translocation of oxygen from shoot to root, of root behavior with reference to soil microorganisms, and of enzymatic activities associated with root growth. In short, a comprehensive program would "comprise several phases of the physiology and ecology of roots, particularly those related to roots as reactive organs of plants" (Cannon 1925a, p. 12). Here again the broader studies never came to fruition; his tendency to examine every aspect of a given problem made for halting progress toward his larger goals.

Nevertheless he chipped away at this comprehensive program until his retirement. Among his major conclusions were that root growth at different oxygen levels is strongly controlled by temperature (Cannon 1923, 1924a, 1925a, b);<sup>40</sup> that there is often a close relation between "the degree of aerobism of a species" and its occurrence in a given habitat (Cannon 1925a, p. 167); that roots could obtain their oxygen supply from one of several sources—directly from the atmosphere, from gases dissolved in soil water or from byproducts of photosynthesis (Cannon 1932a, b, 1940). Continuing his cactus studies, he learned that "roots of *Opuntia* are exceedingly plastic and are directly affected by the immediate condition of the soil environment" (Cannon 1925a, p. 112), and once again confirmed experimentally that cacti are mainly restricted to regions of summer rainfall because they cannot extract water from cool soils (Cannon 1925a).

During the twenties and thirties, Cannon broke new physiological ground. He was apparently the first to study rates of root growth under varying temperature and aeration regimes. He was unique in emphasizing root adjustment to local conditions, and in correlating habitat with specific oxygen requirements. While most of his colleagues concentrated on crops and agronomic aspects of root growth (Aung 1974), he experimented with native plants.

By 1923, Cannon felt he needed more extensive research facilities. He thought that Stanford University might cooperate with the Carnegie Institution in establishing and maintaining a laboratory especially designed for root experiments. G. J. Peirce, the Stanford plant physiologist, was interested in the idea, Cannon told MacDougal, and added, "I am certain that such a branch laboratory will



do no harm to this Department and close contact with a strong department of botany as they have at Stanford may be of much use.”<sup>41</sup>

MacDougal disagreed. “The Institution has no honorary or inactive memberships,” he informed Cannon. Furthermore, he did not believe that the institution could be induced to fund a cooperative laboratory such as Cannon proposed.<sup>42</sup> Communication between the two men deteriorated from this point. MacDougal, pulling rank, told Cannon, “It would be advisable for you to devote your energy this year chiefly to finishing up the experimental and literary work on your experiments with roots. . . . The South African work might well go over [into next year] and be finished at your convenience.”<sup>43</sup> Cannon acceded, but five months later he tendered his resignation, to be effective 31 December 1924.<sup>44</sup>

It is difficult now to reconstruct the exact cause of their dispute. Perhaps MacDougal regarded Cannon’s attempt to set up a separate laboratory as insubordination, or he may have been angry with Cannon for not progressing more rapidly with his root research. In any case, Cannon evidently remained at the Coastal Laboratory into 1925, probably to see *Physiological Features of Roots* through publication. The following year he took up a position at Stanford as a lecturer in botany. Although no longer attached to either the Desert Laboratory or the Coastal Laboratory, he remained a research associate with the Carnegie Institution through 1934.<sup>45</sup>

Even this was apparently more than MacDougal could stomach, for he tried to force Cannon out of the institution entirely in 1926. Burton Livingston, their mutual friend, was against this move and said so to Forrest Shreve: “I regard Cannon’s last publication [*Physiological Features of Roots*, in all likelihood] as just as good as anything that has ever come from the department. . . . In his earlier work on roots C. opened the field and stands very high in my estimation.” Cannon had been with the Carnegie Institution longer than any other botany worker, Livingston pointed out, “and some valid reason for his being dropped ought to be given, something besides general incompetence, for we know that is not a reason in this case.”<sup>46</sup>

During retirement, Cannon returned to his early interest in classification of root systems (Cannon 1949, 1954). “A system of classification should be helpful in comparing the root systems of genetically diverse plants growing in a single habitat as well as those of genetically uniform stock which differ because of unlike environmental conditions,” he wrote (Cannon 1949, p. 542). His classification scheme, which described and illustrated six primary and four adventitious types of root systems, has been called a classic (Zobel 1975). Ludwig (1977) found it “simple and workable” and suggested only minor modifications to suit it to a more quantitative age.<sup>47</sup>



When he died on 16 January 1958, Cannon had been largely forgotten by ecologists and physiologists alike. No obituaries appeared in the major journals and even the Carnegie Institution failed to note his passing in its yearbook. In earlier years, he had been well-known in his field; from 1910 to 1944, he was starred in *American Men of Science*, an indication that his colleagues ranked him among the top 1000 scientists in the nation. Today his reputation in ecological circles has been eclipsed by Shreve's.<sup>48</sup> Had Cannon worked more extensively in North American deserts, his ecological work might be better known. Shreve, however, effectively pre-empted this niche, which may have been why Cannon pursued desert studies on other continents.

If being the Sonoran Desert's first resident ecologist were Cannon's only claim to fame, he would be worth remembering. As it happens, he was much more. He was one of the first ecologists to take laboratory methodology into the field. He designed and carried out some of the earliest physiological investigations of desert plants, essentially inventing for himself the science of physiological ecology. Cannon was the first plant ecologist to discuss competition in deserts and the first to demonstrate that cacti are most prevalent in regions of summer rainfall because their roots cannot absorb water from cold soils. Although Volkens, Kerner, and Schimper (Oppenheimer 1960) anticipated him in Old World deserts, Cannon was among the earliest plant ecologists to investigate xeromorphic adaptation in the American desert. Moreover, he seems to have been *the* first plant ecologist to evaluate the influence of family characters on xeromorphic life-forms. He pioneered not just in the ecology of desert root systems but in the root system as an object of botanical inquiry at many levels; as Livingston said, "C. opened up the field." As Cannon narrowed his field of interest from roots in general to roots in the laboratory, he continued to make novel and worthwhile contributions, chief among them the reciprocal effect of oxygen and temperature on root growth.

His career as a whole showed an alternating pattern of going wide and going deep, of ecological broadening and physiological delving. His major research, the root work, enabled him to burrow deeply into a narrow topic, and his minor research, desert plant ecology, let him dabble in the broader issues of speciation, diversity, and adaptation. Because his training made him most comfortable with experimental studies, his best work in ecology was always firmly grounded in physiology and anatomy. He thought of himself as a physiological ecologist (Cannon 1921); today we might be more likely to classify him as an ecological physiologist.

If, rather sadly, his relationship with MacDougal soured toward the end, his long association with the Carnegie Institution was, on the whole, profitable for both the institution and the man. As Cannon



himself told MacDougal in 1905, “[The Desert Laboratory] will be one of the leading botanical stations in the world; I am proud to be an associate in the work.”<sup>49</sup>

#### ACKNOWLEDGMENTS

I thank Joseph Ewan, Susan Conard, Steven P. McLaughlin, James W. O’Leary, Tony L. Burgess, Raymond M. Turner, and Joan Tweit for reviewing the manuscript; Susan Vasquez, Carnegie Institution of Washington, and Margaret Kimball, Stanford University, for their assistance in tracking down certain crucial dates in Cannon’s life; and the Arizona Historical Society and University of Arizona Library Special Collections for access to their archives.

#### NOTES

AHS—Daniel T. MacDougal Papers, Arizona Historical Society, Tucson.

SC—Desert Laboratory Papers, Special Collections, University of Arizona Library, Tucson.

<sup>1</sup> The name “Desert Botanical Laboratory” was quietly replaced with “Desert Laboratory” around 1908. No written explanation for the change has come to light.

<sup>2</sup> Wilder (1967), McGinnies (1981), McIntosh (1983), and Bowers (1990) provide more information about the founding and subsequent history of the Desert Laboratory.

<sup>3</sup> McIntosh (1976), Cittadino (1980) and Tobey (1981) document the early years of American plant ecology.

<sup>4</sup> W. A. Cannon to D. T. MacDougal, 21 Sep 1903, AHS.

<sup>5</sup> W. A. Cannon to D. T. MacDougal, 2 Nov 1903, AHS.

<sup>6</sup> W. A. Cannon to D. T. MacDougal, 23 Oct 1903, AHS.

<sup>7</sup> W. A. Cannon to D. T. MacDougal, 10 Dec 1903, AHS. Cannon later turned this work over to Effie Spalding, Volney Spalding’s wife (Spalding 1905).

<sup>8</sup> W. A. Cannon to D. T. MacDougal, 2 Dec 1903, AHS.

<sup>9</sup> W. A. Cannon to D. T. MacDougal, 17 May 1904, AHS.

<sup>10</sup> W. A. Cannon to D. T. MacDougal, 22 Feb 1905, AHS.

<sup>11</sup> W. A. Cannon to D. T. MacDougal, 15 Sep 1903, AHS.

<sup>12</sup> W. A. Cannon to D. T. MacDougal, 13 Jun 1904, AHS.

<sup>13</sup> W. A. Cannon to D. T. MacDougal, 18 Aug 1904, AHS.

<sup>14</sup> F. V. Coville to D. T. MacDougal, 12 Jul 1904, AHS.

<sup>15</sup> W. A. Cannon to D. T. MacDougal, 24 Oct 1904, AHS.

<sup>16</sup> F. V. Coville to W. A. Cannon, 3 Oct 1904, AHS.

<sup>17</sup> D. T. MacDougal to W. A. Cannon, 16 Aug 1905, AHS.

<sup>18</sup> W. A. Cannon to D. T. MacDougal, 21 Dec 1905, AHS.

<sup>19</sup> R. S. Woodward to W. A. Cannon, 1 Mar 1905, AHS.

<sup>20</sup> W. A. Cannon to R. S. Woodward, 8 Mar 1905, AHS.

<sup>21</sup> W. A. Cannon to D. T. MacDougal, 11 Jan 1911, AHS.

<sup>22</sup> Cannon was not the first scientist to investigate the root systems of desert plants: Preston had already excavated five cactus species near Tucson and discovered the heteromorphic root system characteristic of many cacti (Preston 1900).

<sup>23</sup> This method, which emphasized the horizontal spread of roots, may not have provided adequate information on their vertical profile. Weaver (1919), in excavating roots of prairie plants to depths of six meters, emphasized equally their vertical and horizontal distribution.

<sup>24</sup> Cannon’s classification of cactus root systems relied on a limited number of species. Gibson and Nobel (1986), in classifying the root systems of North and South American cacti, found five common patterns.

<sup>25</sup> Yeaton et al. (1977) confirmed and extended Cannon’s results. They demon-



strated effects of competition on plant size and discovered interspecific competition between several species pairs.

<sup>26</sup> Barbour challenged Cannon's conclusions about competition: Cannon's own data showed that "there may be considerable space between root systems as well as overlap of roots of close neighbors," he wrote (Barbour 1973, p. 46).

<sup>27</sup> D. T. MacDougal to W. A. Cannon, ca. Aug 1908, AHS.

<sup>28</sup> D. T. MacDougal to W. R. Dudley, 18 Nov 1910, AHS. The logical place to extend their work would have been northern Mexico, but political turmoil, culminating in the revolution of 1911, had made the border region unsafe for travelers.

<sup>29</sup> These censuses were simply tallies of individuals for each species present. The value of this data seems dubious as Cannon did not integrate it into his discussion of vegetation and environment. Plant censuses had been recently popularized by Clements (1905, 1907), and it seems likely that Cannon undertook them in the belief that they were a necessary and proper activity of plant ecologists.

<sup>30</sup> Cannon later noted that succulents reach their best development in regions of moderate rainfall, extending only a short distance into drier and wetter regions (Cannon 1924a). Their distribution, in other words, is correlated less with season of rainfall than total rainfall. This point has been corroborated with abundant detail by Burgess and Shmida (1988).

<sup>31</sup> W. A. Cannon to D. T. MacDougal, 3 May 1917, AHS.

<sup>32</sup> W. A. Cannon to D. T. MacDougal, 13 May 1916, AHS.

<sup>33</sup> D. T. MacDougal to G. Sykes, 13 Jul 1917, AHS.

<sup>34</sup> W. A. Cannon to D. T. MacDougal, 1 Jul 1918, AHS.

<sup>35</sup> W. A. Cannon to D. T. MacDougal, 22 Aug 1918, AHS.

<sup>36</sup> Cannon may have consciously or unconsciously borrowed this value of 0.15 inch from Forrest Shreve, who estimated that at the Desert Laboratory, "the lower limit of significant rainfalls may be placed at 0.15 in" (Shreve 1917, p. 21).

<sup>37</sup> Cannon oversimplified the problem of leaf reduction. Small leaves are more efficient than large ones in dissipating heat, thus are able to maintain temperatures closer to that of the air (Gates 1968; Gates et al. 1968). A major benefit of lowered leaf temperature for desert plants is reduced transpiration per unit of leaf area (Smith 1978).

<sup>38</sup> The topic of leaf morphology in relation to climate was then beginning to receive the attention of ecologists (Parkhurst and Loucks 1972). Cannon did not cite such contemporaries as Bailey and Sinnott (1916) or Brown (1919), presumably because he was unfamiliar with their work.

<sup>39</sup> Cannon may have taken this list of xeromorphic adaptations from Schimper (1903), who may in turn have gotten it from Volken (Oppenheimer 1960).

<sup>40</sup> Although Vlamis and Davis (1944) call the oxygen studies presented in *Physiological Features of Roots* "indecisive," other colleagues cited the book frequently—for example, Weaver and Bruner (1927) and Miller (1938).

<sup>41</sup> W. A. Cannon to D. T. MacDougal, 9 Feb 1923, SC.

<sup>42</sup> D. T. MacDougal to W. A. Cannon, 13 Feb 1923, SC.

<sup>43</sup> D. T. MacDougal to W. A. Cannon, 30 Mar 1923, SC.

<sup>44</sup> W. A. Cannon to D. T. MacDougal, 4 Sep 1923, SC. According to Carnegie Institution records, he retired officially from the staff on 1 Jan 1925.

<sup>45</sup> During this period, at least some of his research was funded by the American Association for the Advancement of Science and the National Research Council.

<sup>46</sup> B. E. Livingston to F. Shreve, 2 Feb 1926, SC.

<sup>47</sup> Drew (1979) pointed out that root classification systems generally suffer from oversimplification, since environmental factors often override root morphology to such an extent that a given root system fails to conform to any of the classified types. Moreover, he noted that among ten types of root systems described for Near Eastern plants, none matched Cannon's types.

<sup>48</sup> Only Nobel (1988) has paid more than passing attention to Cannon's research, and he restricted himself to Cannon's work on cacti.

<sup>49</sup> W. A. Cannon to D. T. MacDougal, 21 Dec 1905, AHS.



## LITERATURE CITED

- AUNG, L. H. 1974. Root-shoot relationships. Pp. 29–61 in E. W. Carson (ed.), *The plant root and its environment*. University Press of Virginia, Charlottesville.
- BAILEY, I. W. and E. W. SINNOTT. 1916. The climatic distribution of certain types of angiosperm leaves. *Amer. J. Bot.* 3:24–39.
- BARBOUR, M. G. 1973. Desert dogma reexamined: root/shoot productivity and plant spacing. *Amer. Midl. Naturalist* 89:41–57.
- BOWERS, J. E. 1988. *A sense of place: the life and work of Forrest Shreve*. University of Arizona Press, Tucson.
- . 1990. *A debt to the future: scientific achievements of the Desert Laboratory, Tumamoc Hill, Tucson, Arizona*. Desert Plants (in press).
- BROWN, W. H. 1919. *Vegetation of Philippine mountains: the relation between environment and physical types at different altitudes*. Bureau of Science Publication no. 13. Department of Agriculture and Natural Resources, Manila.
- BURGESS, R. L. 1977. The Ecological Society of America: historical data and some preliminary analyses. Pp. 1–24 in F. N. Egerton and R. P. McIntosh (eds.), *History of American ecology*. Arno Press, New York.
- BURGESS, T. L. and A. SHMIDA. 1988. Succulent growth-forms in arid environments. Pp. 383–395 in E. E. Whitehead, C. F. Hutchinson, B. N. Timmermann, and R. G. Varady (eds.), *Arid lands today and tomorrow: proceedings of an international research and development conference*. Westview Press, Boulder, CO.
- CARNEGIE YEARBOOK. 1902–1940. Vols. 1–39. Carnegie Institution of Washington, Washington, DC.
- CITTADINO, E. 1980. Ecology and the professionalization of botany in America, 1890–1902. *Studies in the History of Biology* 4:171–198.
- CLEMENTS, F. E. 1905. *Research methods in ecology*. University Publishing Company, Lincoln, NE.
- . 1907. *Plant physiology and ecology*. Henry Holt, New York.
- DREW, M. C. 1979. Root development and activities. Pp. 573–606 in D. W. Goodall and R. A. Perry (eds.), *Arid-land ecosystems*, Vol. 1. Cambridge University Press, Cambridge.
- FELDMAN, L. J. 1988. The habits of roots. *BioScience* 38:612–618.
- GATES, D. M. 1968. Transpiration and leaf temperatures. *Annual Rev. Pl. Physiol.* 19:211–238.
- , R. ALDERFER, and E. TAYLOR. 1968. Leaf temperatures of desert plants. *Science* 159:994–995.
- GIBSON, A. C. and P. S. NOBEL. 1986. *The cactus primer*. Harvard University Press, Cambridge, MA.
- LAWRENCE, D. B. 1948. Introduction. *Ecology* 29:227–229.
- LUDWIG, J. A. 1977. Distributional adaptations of root systems in desert environments. Pp. 85–91 in J. K. Marshall (ed.), *The belowground ecosystem: a synthesis of plant-associated processes*. Department of Range Science, Colorado State University, Fort Collins, CO.
- MACDOUGAL, D. T. 1903. Some aspects of desert vegetation. *Pl. World* 6:249–257.
- MCGINNIES, W. G. 1981. *Discovering the desert: legacy of the Carnegie Desert Botanical Laboratory*. University of Arizona Press, Tucson.
- MCINTOSH, R. P. 1976. Ecology since 1900. Pp. 353–372 in B. J. Taylor and T. J. White (eds.), *Issues and ideas in America*. University of Oklahoma Press, Norman.
- . 1983. Pioneer support for ecology. *BioScience* 33:107–112.
- MILLER, E. C. 1938. *Plant physiology*. McGraw-Hill, New York.
- NOBEL, P. S. 1988. *Environmental biology of agaves and cacti*. Cambridge University Press, Cambridge.
- OPPENHEIMER, H. R. 1960. Adaptation to drought: xerophytism. Pp. 105–138 in *Plant-water relationships in arid and semi-arid conditions: reviews of research*. UNESCO, Paris.



- PARKHURST, D. F. and O. L. LOUCKS. 1972. Optimal leaf size in relation to environment. *J. Ecol.* 60:505–537.
- PRESTON, C. E. 1900. Observations on the root systems of certain Cactaceae. *Bot. Gaz.* (Crawfordsville) 30:348–351.
- SCHIMPER, A. F. W. 1903. Plant-geography upon a physiological basis. Clarendon Press, Oxford.
- SEARS, P. B. 1956. Some notes on the ecology of ecologists. *Sci. Monthly* 83:22–27.
- SHREVE, F. 1911. The influence of low temperatures on the distribution of the giant cactus. *Pl. World* 14:136–146.
- . 1915. Vegetation of a desert mountain range as conditioned by climatic factors. Carnegie Institution of Washington Publication no. 217. Carnegie Institution of Washington, Washington, DC.
- . 1917. The establishment of desert perennials. *J. Ecol.* 5:210–216.
- . 1936. Plant life of the Sonoran Desert. *Sci. Monthly* 42:195–213.
- SMITH, W. K. 1978. Temperatures of desert plants: another perspective on the adaptability of leaf size. *Science* 201:614–616.
- SPALDING, E. S. 1905. Mechanical adjustment of the saguaro (*Cereus giganteus*) to varying amounts of water. *Bull. Torrey Bot. Club* 32:57–68.
- SPALDING, V. M. 1904. Biological relations of certain desert shrubs. I: The creosote bush (*Covillea tridentata*) in its relation to water supply. *Bot. Gaz.* (Crawfordsville) 38:122–138.
- TOBEY, R. C. 1981. Saving the prairies: the life cycle of the founding school of American plant ecology, 1895–1955. University of California Press, Berkeley.
- VLAMIS, J. and A. R. DAVIS. 1944. Effects of oxygen tension on certain physiological responses of rice, barley and tomato. *Pl. Physiol.* (Lancaster) 19:33–51.
- WEAVER, J. E. 1919. The ecological relations of roots. Carnegie Institution of Washington Publication no. 286. Carnegie Institution of Washington, Washington, DC.
- . 1926. Root development of field crops. McGraw-Hill, New York.
- and W. A. BRUNER. 1927. Root development of vegetable crops. McGraw-Hill, New York.
- WILDER, J. C. 1967. The years of a desert laboratory. *Arizona Hist.* 8:179–199.
- YEATON, R. I., J. TRAVIS, and E. GILINSKY. 1977. Competition and spacing in plant communities: the Arizona Upland association. *J. Ecol.* 65:587–595.
- ZOBEL, R. W. 1975. The genetics of root development. Pp. 261–274 in J. G. Torrey and D. T. Clarkson (eds.), *The development and function of roots*. Academic Press, New York.

#### PUBLICATIONS OF WILLIAM A. CANNON

Note: An asterisk indicates literature cited in the text.

- 1900a. A morphological study of the flower and embryo of the wild oat, *Avena fatua* L. *Proc. Calif. Acad. Sci.* 1:329–335.
- 1900b. The gall of the Monterey pine. *Amer. Naturalist* 34:801–810.
- \*1901a. On the relation of the redwoods and fog to the general precipitation in the redwood belt of California. *Torrey* 1:137–139.
- \*1901b. A note on the bladder kelp, *Nereocystis luetkeana*. *Torrey* 1:49–52.
- 1901c. The anatomy of *Phoradendron villosum*. *Bull. Torrey Bot. Club* 28:374–390.
- \*1902a. A cytological basis for the Mendelian laws. *Bull. Torrey Bot. Club* 29:657–661.
- 1902b. Field notes on *Rhododendron catawbiense*. *Torrey* 2:161–169.
- \*1903a. Studies in plant hybrids: the spermatogenesis of hybrid cotton. *Bull. Torrey Bot. Club* 30:133–172.
- \*1903b. Studies in plant hybrids: the spermatogenesis of hybrid peas. *Bull. Torrey Bot. Club* 30:519–543.
- \*1904a. Some cytological aspects of hybrids. *Mem. Hort. Soc. New York* 1:89–92.



- \*1904b. Observations on the germination of *Phoradendron villosum* and *P. californicum*. Bull. Torrey Bot. Club 31:435–443.
- \*1905a. A new method of measuring the transpiration of plants in place. Bull. Torrey Bot. Club 32:515–529.
- \*1905b. On the transpiration of *Fouquieria splendens*. Bull. Torrey Bot. Club 32:397–414.
- 1905c. On the water-conducting systems of some desert plants. Bot. Gaz. (Crawfordsville) 39:397–408.
- \*1906a. Two miles up and down in an Arizona desert. Pl. World 9:49–55.
- \*1906b. Biological relations of certain cacti. Amer. Naturalist 40:27–46.
- \*1906c. The Desert Botanical Laboratory of the Carnegie Institution of Washington. Out West 24:25–38.
- 1906d. A curious cactus fruit. Torreya 5:216–217.
- 1906e. The effects of high relative humidity on plants. Torreya 6:21–25.
- 1907. An electric thermoregulator for paraffine baths and incubators. Pl. World 10:262–264.
- \*1908a. The topography of the chlorophyll apparatus in desert plants. Carnegie Institution of Washington Publication no. 98. Carnegie Institution of Washington, Washington, DC.
- \*1908b. On the electric resistance of solutions of salt plants and solutions of alkali soils. Pl. World 11:10–14.
- \*1908c. On the origin of structures in plants. Amer. Naturalist 42:779–782.
- 1908d. A redwood sport. Pl. World 11:232–234.
- \*1909a. Studies in heredity as illustrated by the trichomes of species and hybrids of *Juglans*, *Oenothera*, *Papaver* and *Solanum*. Carnegie Institution of Washington Publication no. 117. Carnegie Institution of Washington, Washington, DC.
- \*1909b. The root system of *Cereus giganteus*. Pp. 59–66 in V. M. Spalding, Distribution and movements of desert plants. Carnegie Institution of Washington Publication no. 113. Carnegie Institution of Washington, Washington, DC.
- \*1909c. The parasitism of *Orthocarpus purpurascens* Benth. Pl. World 12:259–261.
- \*1910a. The root habits and parasitism of *Krameria canescens* Gray. Pp. 5–24 in D. T. MacDougal and W. A. Cannon, The condition of parasitism in plants. Carnegie Institution of Washington Publication no. 129. Carnegie Institution of Washington, Washington, DC.
- 1910b. Travel notes: rural England. Pl. World 13:259–266.
- \*1911. The root habits of desert plants. Carnegie Institution of Washington Publication no. 131. Carnegie Institution of Washington, Washington, DC.
- \*1912a. Deciduous rootlets of desert plants. Science 35:632–633.
- 1912b. Structural relations in xenoparasitism. Amer. Naturalist 46:675–681.
- 1912c. Some features of the root-systems of desert plants. Popular Science Monthly 81:90–99.
- \*1913a. Some relations between root characters, ground water and species distribution. Science 37:420–423.
- \*1913b. Botanical features of the Algerian Sahara. Carnegie Institution of Washington Publication no. 178. Carnegie Institution of Washington, Washington, DC.
- \*1913c. Notes on root variation in some desert plants. Pl. World 16:323–341.
- \*1913d. A note on a chaparral–forest relation at Carmel, California. Pl. World 16:36–38.
- 1914a. On the density of the cell sap in some desert plants. Pl. World 17:209–212.
- \*1914b. Tree distribution in central California. Popular Science Monthly 85:417–424.
- 1914c. Specialization in vegetation and in environment in California. Pl. World 17:223–237.
- 1914d. A note on the reversibility of the water reaction in a desert liverwort. Pl. World 17:261–265.



- \*1915a. On the relation of root growth and development to the temperature and aeration of the soil. *Amer. J. Bot.* 2:211–224.
- 1915b. A manometer method of determining the capillary pull of soils. *Pl. World* 18:11–13.
- \*1916. Distribution of the cacti with especial reference to soil temperature and soil moisture. *Amer. Naturalist* 50:435–442.
- \*1917a. Relation of the rate of root growth in seedlings of *Prosopis velutina* to the temperature of the soil. *Pl. World* 20:320–333.
- 1917b. Soil temperature and plant growth [review]. *Pl. World* 20:361–363.
- \*1917. (with E. E. Free.) The ecological significance of soil aeration. *Science* 45:178–180.
- \*1918. The evaluation of the soil temperature factor in root growth. *Pl. World* 21:64–67.
- 1919. Rainfall and plant distribution in Australia [review]. *Pl. World* 22:19–23.
- \*1920. The ecological relations of roots [review]. *Science* 51:393–394.
- \*1921. Plant habits and habitats in the arid portions of South Australia. Carnegie Institution of Washington Publication no. 308. Carnegie Institution of Washington, Washington, DC.
- \*1923. The influence of the temperature of the soil on the relation of roots to oxygen. *Science* 58:331–332.
- \*1924a. General and physiological features of the vegetation of the more arid portions of southern Africa, with notes on the climatic environment. Carnegie Institution of Washington Publication no. 354. Carnegie Institution of Washington, Washington, DC.
- 1924b. A note on the relation of root-growth in the soil to the oxygen supply: the growth ratio. *Ecology* 5:319–321.
- \*1925a. Physiological features of roots with especial reference to the relations of roots to the aeration of the soil. Carnegie Institution of Washington Publication no. 368. Carnegie Institution of Washington, Washington, DC.
- \*1925b. On the upper critical concentration of oxygen in root growth. *Science* 61:118–120.
- 1930. (with G. F. Beardsley.) Notes on the effects of a mud-flow at Mt. Shasta on the vegetation. *Ecology* 11:326–336.
- \*1932a. On the variation of the oxygen content of cultural solutions. *Science* 75:108–109.
- \*1932b. Absorption of oxygen by roots when the shoot is in darkness or in light. *Pl. Physiol. (Lancaster)* 7:673–684.
- 1933. (with D. Demaree and E. A. Purer.) Evaporation, transpiration and oxygen consumption by roots. *Science* 78:388–399.
- 1935. (with E. A. Purer.) On the removal of oxygen from water by cut branches. *Science* 81:100.
- \*1940. Oxygen relations in hydrophytes. *Science* 91:43–44.
- \*1949. A tentative classification of root systems. *Ecology* 30:542–548.
- \*1954. A note on the grouping of lateral roots. *Ecology* 35:293–295.

(Received 5 Apr 1989; revision accepted 15 Sep 1989.)



# TRICHOME PATTERNS AND GEOGRAPHIC VARIATION IN *LEPTODACTYLON CALIFORNICUM* (POLEMONIACEAE)

PATRICIA J. GORDON-REEDY  
ERC Environmental and Energy Services Co.,  
San Diego, CA 92121

## ABSTRACT

Morphological investigations of *Leptodactylon californicum* revealed several distinct trichome types and patterns of trichome distribution among mostly allopatric geographic races of this species. Furthermore, pubescence characters correlate with discrete geographical regions. Some differences in leaf morphology were also noted, and correlate with trichome patterns and geographical distributions. Morphological variation, in conjunction with geographical distribution, is sufficient to warrant the recognition of five subspecific taxa. The two existing subspecies names, *californicum* and *glandulosum*, are retained, and three new subspecies, **brevitrichomum**, **tomentosum**, and **leptotrichomum**, are recognized.

*Leptodactylon californicum* (Polemoniaceae) is a subshrub endemic to southern California. Its distributional range extends from San Luis Obispo Co. to northern San Diego Co. (Fig. 1). The species occurs from near sea level to about 1550 m in several vegetative associations that include chaparral, an oak woodland/chaparral transitional zone, coastal sage scrub, and coastal strand. Within the species' range, coastal strand habitat is the most divergent with respect to the ecological distribution of the species. This habitat is composed largely of stabilized sand dunes, characterized by a lower annual precipitation than other areas, and subject to sand blast and salt spray. Throughout the range, plants vary with respect to habit, floral color and size, vestiture, and number of leaf divisions. The possible correlation of geographic distributions with patterns of morphological variation presents an intriguing problem within this group. The primary purpose of my study was to investigate variation within *L. californicum* and to determine its taxonomic and evolutionary significance.

*Previous studies.* Systematic work has been conducted sporadically on *L. californicum* since it was named by Hooker and Arnott (1839). Mason (1951) published the most detailed study of the species to date. *Leptodactylon californicum* is a distinct species that is readily circumscribed, but variation has been noted at the subspecific level. Eastwood (1904) recognized *Gilia californica* Benth. subsp. *glandulosa*, based primarily on the presence of glandular trichomes on leaves. Munz (1959) described some distributional and elevational trends, and noted considerable overlap between the subspecies. Ac-



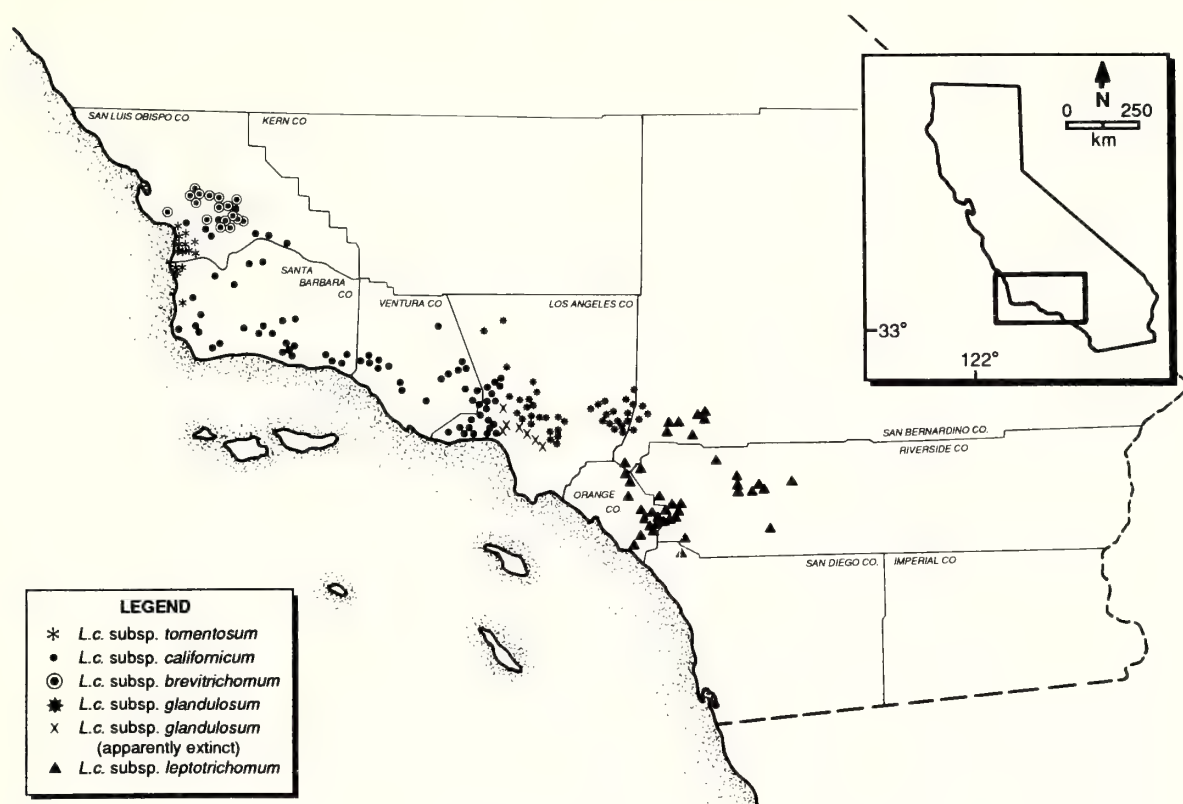


FIG. 1. Distribution of *Leptodactylon californicum* in California.

cording to Munz, subsp. *glandulosum* is restricted to below 3000 ft (914 m) in the San Gabriel, San Bernardino, and Santa Ana mts., whereas subsp. *californicum* occurs below 5000 ft (1524 m) and ranges from San Luis Obispo Co. to the western San Gabriel and Santa Ana mts.

## MATERIALS AND METHODS

**Morphology.** Measurements of floral and vegetative characters were made using field collections (1980–1982) and 390 dried plant specimens. Five measurements were taken per specimen for each character; the number of specimens examined varied among subspecies based on the amount of collected material available. Eleven populations were studied (Table 1). Twenty-four morphological characters were examined for descriptive purposes and 14 of these were identified as potentially useful taxonomic characters (Gordon 1983). Only trichomes and leaf division number proved to be taxonomically significant at the infraspecific level.

Trichomes were examined with an ETEC Autoscan Model U-1 scanning electron microscope (SEM). Leaves, calyces, and stems were field-collected, fixed in FAA, critical-point dried using a Bomar SPC-900/EX Critical Point Dryer, and mounted onto a specimen stub with double-stick adhesive tape. All material was then coated with gold-palladium (60%:40%) using a Technics Hummer V Sputter-coater in preparation for SEM observation.



TABLE 1. SUMMARY OF PREDOMINANT TRICHOME TYPE, DENSITY, AND DISTRIBUTION FOR ELEVEN POPULATIONS OF *LEPTODACTYLON CALIFORNICUM*. \* Intermediate = long, stout trichome type and long, slender trichome type; \*\* = population apparently extinct.

| Taxon                        | Population location   | Trichome type   | Trichome distribution pattern |          |          |
|------------------------------|---|---|-------------------------------|----------|----------|
|                              |   |   | Leaves                        | Stem     | Calyx    |
| subsp. <i>brevitrichomum</i> | La Panza Range  | straight, short (1-4 cells), glandular                    | sparse                        | sparse   | sparse   |
| subsp. <i>leptotrichomum</i> | Santa Ana Mts.  | straight, medium to long (5-12 cells), slender, glandular | sparse to moderate            | moderate | moderate |
| subsp. <i>leptotrichomum</i> | San Bernardino, San Jacinto mts.                                      | intermediate, * glandular                                 | moderate                      | moderate | moderate |
| subsp. <i>glandulosum</i>    | San Gabriel Mts., Los Angeles Basin, ** E Santa Monica Mts. **        | straight, long (8 + cells), stout, glandular              | dense                         | dense    | dense    |
| subsp. <i>californicum</i>   | San Rafael, Santa Ynez, Santa Susana, Santa Monica mts.; Ventura area | wavy (tomentose), eglandular                              | glabrous                      | dense    | moderate |
| subsp. <i>tomentosum</i>     | Coastal strand  | wavy (tomentose), eglandular                              | sparse                        | dense    | dense    |



*Reproductive biology.* Approximately 18 plants of *L. californicum* from six populations throughout the species range were collected during Spring 1981 and maintained in the SFSU greenhouse. Controlled cross-pollinations (Gordon 1983) were made to assess cross-compatibility among different populations. Compatibility between plants was measured by the formation of a capsule upon controlled pollination. Reduced capsule length and lower seed set per capsule were assumed to indicate incipient reproductive barriers. The ability to successfully cross-breed was tested by chi-square analyses, with significant differences reported for p values less than 0.05 and highly significant differences for p values less than 0.01 (Zar 1974). Differences among crosses in capsule length or number of seed produced per capsule were tested by analysis of variance, with the same significance levels.

## RESULTS

*Morphology.* The trichomes of *L. californicum* occur in different combinations of size, pattern, and density in different populations (Fig. 2). Trichomes are typically slender and multicellular, but differ in number of cells and the presence or absence of an apical gland. Individual trichome cells are hyaline and slightly constricted at each end. They are generally longer than wide and more or less cylindrical (Fig. 2). Trichome morphology of greenhouse-maintained plants did not vary from parental types, and this suggests that they are a taxonomically stable character within *L. californicum*.

Four main trichome "types" are readily discernible in *L. californicum* (Fig. 2). Individual trichomes of each type can be described as short, straight, and glandular; medium to long, straight, slender, and glandular; long, straight, stout, and glandular; and wavy and eglandular. It should be emphasized that these types represent the dominant form of trichome that occurs within each subspecies. It is common to find other trichome types present at a lesser density, but type and distribution circumscribe each taxon (Table 1).

The short, glandular trichomes of specimens of subsp. *brevitrichomum* of the southern La Panza, Santa Lucia, and San Luis ranges occur on leaves, calyces, and stems, but pubescence is extremely sparse on all parts. Plants designated as subsp. *leptotrichomum* from the Santa Ana Mts. have a trichome distribution similar to subsp. *brevitrichomum*, but type and density of trichome is markedly different (Table 1). Trichomes of subsp. *leptotrichomum* are long, slender, glandular or eglandular, and occur in moderate densities on all plant parts. A striking contrast is provided by subsp. *glandulosum* populations of the San Gabriel Mts. where trichomes are long, stout, and glandular, and pubescence is extremely dense on all plant parts. Furthermore, this population has the highest density of glandular



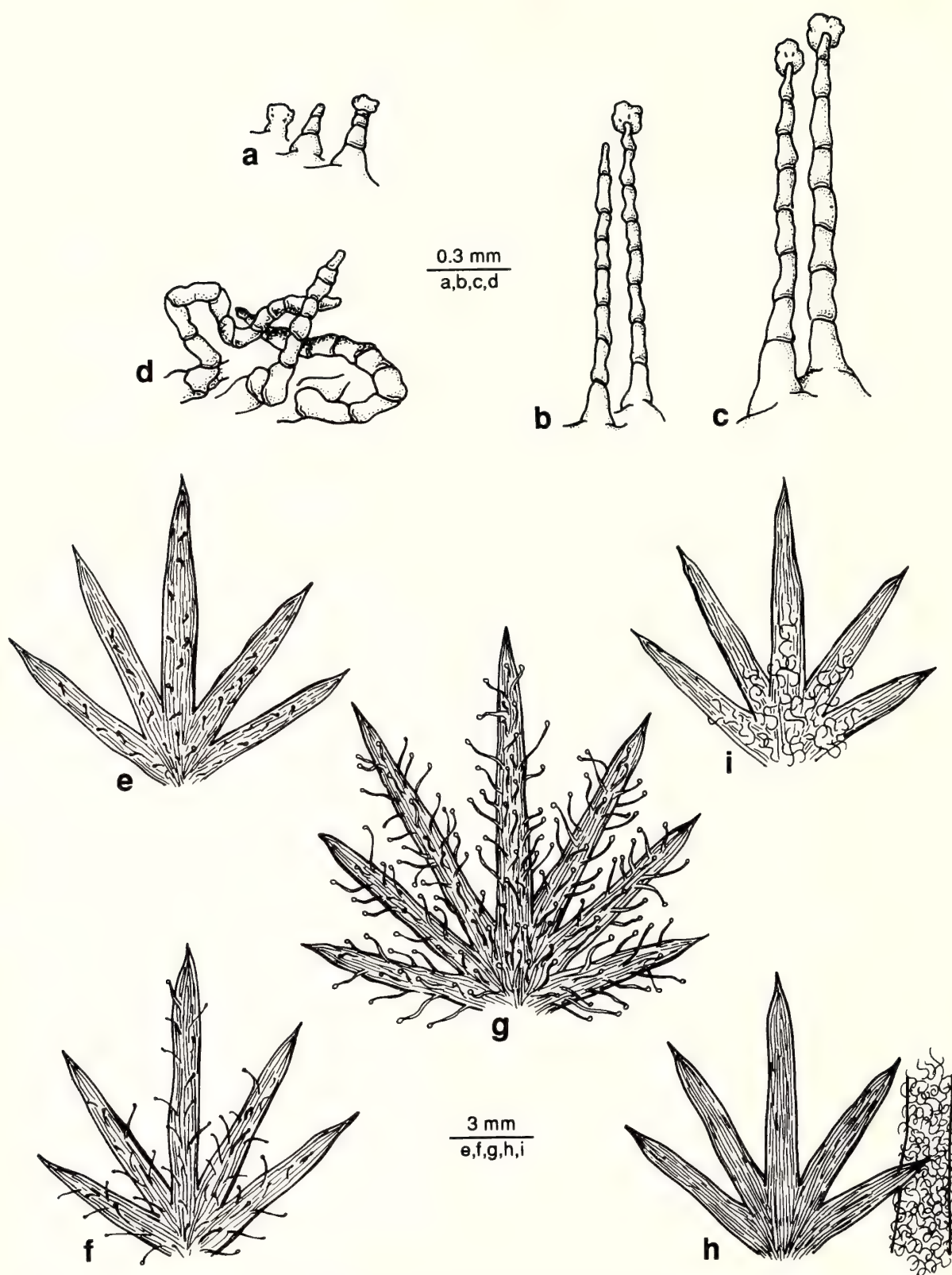


FIG. 2. *Leptodactylon californicum*. a-d. Representative trichome types. a. subsp. *brevitrichomum*. b. subsp. *leptotrichomum*. c. subsp. *glandulosum*. d. subspp. *californicum* and *tomentosum*. e-i. Trichome distribution on leaves (and stem in h). e. subsp. *brevitrichomum*. f. subsp. *leptotrichomum*. g. subsp. *glandulosum*. h. subsp. *californicum* (note glabrous leaves and tomentose stems). i. subsp. *tomentosum*.



trichomes within the species. San Bernardino and San Jacinto mt. populations are intermediate between subsp. *leptotrichomum* (Santa Ana Mts.) and subsp. *glandulosum* with respect to type and density of trichomes. Trichome type is generally slender, although some stout trichomes do occur. In both groups of populations, pubescence occurs on leaves, calyces, and stems, and is often denser than in the Santa Ana Mts., but never approaches the trichome density of plants in the San Gabriel Mts. Thus, these populations are referred to subsp. *leptotrichomum*. Populations referable to subsp. *californicum* are unique in that they possess glabrous (or nearly so) leaves, densely tomentose stems, and moderately tomentose calyces. Populations that occur along the coastal strand are referable to subsp. *tomentosum* in which the tomentum is noticeably denser on stems and calyces, and often occurs scattered on leaves.

The leaves of *L. californicum* are sessile and palmately divided into linear, acerose segments. Leaf division number varies from three to nine, with an uneven number of divisions most common. The majority of populations are dominated by plants with three or five leaf divisions. Plants in the San Gabriel Mts. and the apparently extinct Los Angeles Basin and eastern Santa Monica Mt. populations (subsp. *glandulosum*), however, are noteworthy in that leaf division number ranges from three to nine, with seven and nine divisions being most common (53.1% of leaves have divisions greater than 5;  $n$  [number of leaves measured] = 431). Greater leaf lobe number also is seen occasionally in subsp. *leptotrichomum* in the San Bernardino Mt. population (21.8%;  $n$  = 188), and rarely in the Santa Ana and San Jacinto mts. (1.1%;  $n$  = 454).

*Distribution.* *Leptodactylon californicum* occurs as a series of mostly allopatric geographic races throughout its range (Table 1). Some of these disjunctions appear to have existed for a long time, as evidenced by morphological differentiation and historical records which suggest that no recent connection existed with neighboring populations. Other disjunctions, however, appear to be more recent in origin, often the result of human-related disturbance in the past century such as habitat loss from agriculture or urbanization. Populations which appear to be recently isolated include those from the San Rafael Mts. southward to the western Santa Monica Mts.

*Reproductive biology.* Results of artificial hybridizations show that *L. californicum* exhibits a low level of self-compatibility (successful crosses = 5%; number of attempted crosses [ $n$ ] = 98) (Gordon 1983). Geographically isolated populations generally appear to interbreed readily (73.2%;  $n$  = 713). Exceptions are as follows. Crosses between plants of La Panza Range population (pistillate parent) and the San Jacinto Mt. population (staminate parent) were unsuccessful (0.0%;  $n$  = 5), although the small sample size may be a factor. The reciprocal



crosses (i.e., San Jacinto Mt. plants = pistillate parent; La Panza Range plants = staminate parent) did result in a high level of capsule formation (85.7%;  $n = 7$ ), but a highly significant reduction in capsule length ( $\bar{x} = 5.87$  mm;  $p < 0.01$ ) and/or number of seeds set per capsule (6.67 seeds/capsule;  $p < 0.01$ ) compared to other crosses using plants from the San Jacinto Mts. as the pistillate parent (Gordon 1983). There also appears to be a unidirectional reduction in crossability between subsp. *glandulosum* (pistillate parent) of the San Gabriel Mts. and subsp. *leptotrichomum* (staminate parent) of the Santa Ana Mts. (63.6%;  $n = 77$ ), but no significant differences in capsule length or seed set per capsule in successful crosses. The reciprocal cross, using subsp. *leptotrichomum* as the pistillate parent, indicates a high level of crossability (87.1%;  $n = 62$ ). These limited hybridization studies are most valuable in emphasizing the close genetic relationships among subspecies of *L. californicum*.

## DISCUSSION

Subspecies recognized in this treatment can be distinguished solely on pubescence characters that apparently are stable within populations. There is precedence for the utility of trichome type and distribution as a taxonomic character in the Polemoniaceae. For example, *Gilia* Ruiz Lopez & Pavón sect. *Arachnion* (Grant 1959) is defined primarily by pubescence; *Eriastrum* Wootton & Standl. is distinguished, in part, from *Navarretia* Ruiz Lopez & Pavón by trichome types (Grant 1959) as is *Langloisia* E. Greene from *Loeseliastrum* (Brand) Timbrook (Timbrook 1986); and trichomes have been used at the subspecific level in *Polemonium* L. (Grant 1959) and *Linanthus* Benth. (Patterson 1977). Grant (1959) suggested that a survey of trichome types and their distribution in the family would be of value. My examination of trichomes with the SEM demonstrates that glandularity versus non-glandularity is not per se a valid basis for recognizing subspecies, because all plants appear to possess some glandular trichomes. Rather, it is density of glandular hairs, trichome type (e.g., stout versus slender), and cell number, that is diagnostic.

Another misconception within this group has been that glandular individuals (undoubtedly references to subsp. *glandulosum*) are restricted to the southern part of the range. It is apparent from this study that a north-south trend does not exist, as shown by subsp. *brevitrichomum* from La Panza, Santa Lucia, and San Luis ranges.

Leaf morphology also has been a useful taxonomic character within the Polemoniaceae. Leaf divisions are used, in part, to separate *Polemonium* L. from *Collomia* Nutt., and *Phlox* L. and *Microsteris* E. Greene from *Leptodactylon* Hook. & Arn. and *Linanthus* Benth. The greater leaf division number seen in the southern portion of the



range, particularly within subsp. *glandulosum*, has value in further delimiting taxonomic entities, particularly when used in addition to pubescence characters.

Although glandularity alone is not a basis for separation of *L. californicum* into northern and southern elements, such a division based on pubescence and leaf characters may, in fact, be valid. Two major alliances can be recognized within *L. californicum* based on these features. The first alliance includes subspp. *californicum* and *tomentosum* that possess the same trichome type, glabrous to sparse leaf pubescence, and five or fewer leaf divisions. Subsp. *tomentosum* differs from subsp. *californicum* mainly in density of pubescence. It is convenient to include subsp. *brevitrichomum* in this group based on its geographical proximity, leaf division number, and leaf pubescence density. Subsp. *brevitrichomum* represents an anomalous situation, however, because it displays a markedly different, glandular trichome type (Fig. 2). It appears that the glandular type of subsp. *brevitrichomum* is an independently derived condition.

The southern group, comprising subspp. *leptotrichomum* and *glandulosum*, forms the second alliance, based on moderate to dense leaf pubescence, glandularity, presence of predominantly straight trichomes, and occurrence of a greater number of leaf divisions than in northern populations. Glandularity in this group is characterized by long-stipitate hairs as opposed to the short-stipitate hairs of subsp. *brevitrichomum* in La Panza, Santa Lucia, and San Luis ranges.

It is difficult to ascertain which trichome type is ancestral, or whether the eglandular state is ancestral to the glandular state. Relationships between northern and southern groups are also unclear. Particularly enigmatic is the fairly sharp break and lack of intergradation noted where individuals of subsp. *californicum* and subsp. *glandulosum* occur in proximity, as formerly occurred in the Santa Monica Mts. Although artificial hybridizations were made easily between these subspecies, no intermediates have been found in nature or on herbarium specimens. This suggests an external reproductive barrier. The only apparent ecological difference in this zone of near-sympatry may be soil type, with soils in the northern portion of the Santa Monica Mts. derived from sedimentary material, and soils to the south (and in the San Gabriel Mts.) derived primarily from granitic parental material.

Fragmentation has occurred within this taxon, as evidenced by separation of the species range into isolated, morphologically distinct groups. Interfertility among most populations indicates that reproductive isolation is not yet complete. Reproductive compatibility, in conjunction with varying degrees of morphological differentiation, are suggestive of a once-widespread range. Stebbins (1974) noted that most species are composed of a series of races, and that the distinctiveness of those races determines whether or not they are



deserving of taxonomic recognition. The presence of geographical disjunctions within *L. californicum* that correlate with distinct patterns of variation indicate that subspecific recognition is warranted. Based on the findings of this study, the two existing subspecies, *L. californicum* subsp. *californicum* and *L. californicum* subsp. *glandulosum*, are retained and three other subspecies, *brevitrichomum*, *tomentosum*, and *leptotrichomum*, are recognized.

### TAXONOMIC TREATMENT

#### Key to Subspecies of *Leptodactylon californicum*

- a. Trichomes predominantly glandular; straight.
  - b. Trichomes short (1–4 cells); pubescence sparse; La Panza, Santa Lucia, and San Luis ranges, San Luis Obispo Co. . . . . 1. subsp. *brevitrichomum*
  - b' Trichomes mostly longer (4–12+ cells); pubescence moderate to dense; southern California.
    - c. Pubescence glandular, dense (nearly covering surface of leaves, calyces, and stems); trichomes stout (basal cells to 85  $\mu$ m wide, middle cells 40–75  $\mu$ m wide, apical cell 10–20  $\mu$ m wide); leaf divisions (5–)7–9; San Gabriel Mts., eastern Santa Monica Mts., Los Angeles Co. . . . . 2. subsp. *glandulosum*
    - c' Pubescence mostly glandular with scattered eglandular hairs, sparse to moderate (scattered to partially covering surface of leaves, calyces, and stems); trichomes slender (basal cells to 60  $\mu$ m wide, middle cells 35  $\mu$ m wide, apical cell less than 10  $\mu$ m wide) to occasionally stout; leaf divisions 3–5(–)7; Santa Ana, San Jacinto, and San Bernardino mts. . . . . 3. subsp. *leptotrichomum*
- a' Trichomes predominantly eglandular; pubescence tomentose.
  - d. Stems densely pubescent; calyces moderately pubescent; leaves glabrous; southern San Luis Obispo Co. to Los Angeles Co. . . . . 4. subsp. *californicum*
  - d' Stems and calyces densely pubescent; leaves sparsely to moderately pubescent; Coastal strand, San Luis Obispo and Santa Barbara counties. . . . . 5. subsp. *tomentosum*

**LEPTODACTYLON CALIFORNICUM** Hook. & Arn., Bot. Beechey's Voy. 369.

Subshrub, 3–13 dm high. Stems with glandular or eglandular multicellular trichomes. Leaves alternate, sessile, palmately 3–9 divided into unequal, linear-acerose segments; leaf divisions 3–12 mm long, glabrous or with glandular or eglandular multicellular trichomes. Flowers diurnal, sessile. Calyx lobes 8–16 mm long, equal in length, with glandular or eglandular multicellular trichomes. Corolla salverform; lobes 9–18 mm long, deep pink to light pink, rarely white, fading to lavender or purple, elliptic-obovate to round; tube and throat 9–20 mm long, white to faintly pink or purple. Stamens inserted at mid-tube; filaments 0.5–1.7 mm long; anthers 1.5–4.2 mm long. Capsule ellipsoid to ovate, 2.3–10 mm long. Seeds numerous, 0.8–1.5 mm long, light brown to red-brown or red-black, irregularly angled, mucilaginous when wetted.  $n=9$ . Flowering Dec to Aug(–Sep).

**1. *Leptodactylon californicum* Hook. & Arn. subsp. *brevitrichomum* Gordon subsp. nov.**—TYPE: USA, California, San Luis



Obispo Co., La Panza Range, Hwy. 58, 8 km E of Santa Margarita, 24 Apr 1981, *Gordon* 828 (holotype, CAS; isotypes, GH, LA, MACF, MO, NY, OBI, PH, RSA, SBBG, SFSU, UC, UCSB, US).

Folia 3–5 divisio; caulis calycis et foliorum indumentum sparsum; trichomata brevia, plerumque 1–4 cellulae longae, recta, plerumque glandulifera; corollae 22–37 mm longae, rosiae, aliquando subrosiae.

Leaf divisions 3–5; stems, leaves, and calyces sparsely pubescent; trichomes short, generally 1–4 cells long, straight, predominantly glandular; corollas large, 22–37 mm long, mostly deep pink.

*Paratypes.* San Luis Obispo Co., Lopez Canyon, 4.5 mi above dam site, *Havlik* 127 (OBI); 2 mi W of La Panza, *Keck* 2817 (DS, POM, UC); 10 mi E of Santa Margarita, *Ferris and Rossbach* 9452 (DS, GH, RSA, UC); Pozo–La Panza road, 0.4 mi W of junction with road to Queen Bee Campground, *Gordon* 830 (SFSU).

*Distribution.* Subspecies *brevitrichomum* is abundant in the vicinity of Pozo and Santa Margarita in La Panza Range, and appears scattered in the Santa Lucia and San Luis ranges. This subspecies occurs between 366–700 m in chaparral or occasionally a transitional oak woodland/chaparral community.

Pubescence may appear to be lacking if specimens are not examined closely. The short, glandular leaf trichomes are particularly diagnostic of this taxon. White-flowered specimens have been collected in the region, but corolla color is generally a deep pink or rose, and corollas are large (22–37 mm long). Occasionally, stem trichomes resemble the tomentose form except that they are much shorter (1–4 cells vs. 4–12+ cells). Feb–May.

Two morphs occur in La Panza Range. The common type is characterized by sparse pubescence overall, and by short, glandular leaf trichomes. Plants possessing this trichome pattern are recognized as *L. californicum* subsp. *brevitrichomum*. Individuals ascribable to subsp. *californicum* occasionally occur in the southern end of this range. Evidence of some intergradation exists between these two subspecies in La Panza Range, with individuals displaying leaf pubescence of subsp. *brevitrichomum* but stem pubescence resembling subsp. *californicum* (i.e., trichomes are wavy, but shorter and sparser than true subsp. *californicum*). In this zone of intergradation, which occurs in the vicinity of La Panza Campground, the extreme form of subsp. *brevitrichomum* is also found. Because subsp. *brevitrichomum* is the most common form in La Panza Range, this partial intergradation might reflect a relatively recent northward extension of subsp. *californicum*. The distance between La Panza Range and the nearest population of typical subsp. *californicum* is about 32 km (Cuyama Valley). Although suitable intervening habitat is not now present, it may have been in the recent past. Thus, the intermediate



individuals in the southern portion of the range may represent a relictual contact zone. A few collections ascribable to subsp. *californicum* have also been made in the southern Santa Lucia and San Luis ranges, but no evidence of integradation is apparent.

2. **LEPTODACTYLON CALIFORNICUM** Hook. & Arn. subsp. **GLANDULOSUM** (Eastw.) Mason in Abrams, *Illus. Fl. of the Pacific States* 3:454. 1951.—*Gilia californica* Benth. var. *glandulosa* Eastw., *Bot. Gaz.* 37:447. 1904.—*Leptodactylon californicum* forma *glandulosum* (Eastw.) Wherry, *Amer. Midl. Nat.* 34:383. 1945.—**TYPE:** California, Los Angeles Co., Mt. Wilson, Switzer's Trail, 4 Jul 1904, *F. Grinnell, Jr. s.n.* (holotype, CAS!).

Leaf divisions (5–)7–9; stems, leaves, and calyces densely pubescent; trichomes long, stout (basal cells to 85  $\mu\text{m}$  wide, middle cells 40–75  $\mu\text{m}$  wide, apical cell 10–20  $\mu\text{m}$  wide), straight, predominantly glandular; corollas medium to large, 20–35 mm long, pink.

*Distribution.* Subsp. *glandulosum* was once common in the Los Angeles Basin and eastern Santa Monica Mts., but is now restricted largely to sites below 1524 m in the foothills and western slope of the San Gabriel Mts. Plants of this subspecies are primarily found in association with chaparral, although some populations occur quite close to the lower limits of westside ponderosa pine forest (Holland 1986).

This taxon is the most densely glandular within the species. Stem trichomes are straight, and not tomentose as described by Eastwood (1904). Feb–Aug(–Sep).

The eastern Santa Monica Mt. population is clearly allied with Los Angeles Basin and San Gabriel Mt. populations, rather than the western Santa Monica Mt. population. These distributions suggest that a “corridor” existed from the eastern Santa Monica Mts. (near Topanga Canyon) along the edge of the Los Angeles Basin to the foothills of the San Gabriel Mts. Of these areas, only the San Gabriel Mts. currently supports any substantial stands of *L. californicum*. The San Gabriel Mt. population is distinct from other extant populations with respect to pubescence and leaf characters, with its long, stout trichomes, the greatest density of leaf pubescence and overall glandularity within the species, and leaf lobe number of five to nine.

3. **Leptodactylon californicum** Hook. & Arn. subsp. **leptotrichomum** Gordon subsp. nov.—**TYPE:** USA, California, Orange Co., Santa Ana Mts., Hwy. 74, 0.9 km N of Ortega Oaks National Forest Campground, 2 May 1981, *Gordon 836* (holotype, CAS; isotypes, GH, LA, MACF, MO, NY, OBI, PH, RSA, SBBG, SFSU, UC, UCSB, US).



Folia plerumque 3–5 divisio, aliquando 6–7 divisio; caulis et calycis indumentum moderatum, foliorum moderatum sparsumve; trichomata media longave (5–12 cellulae), gracilia (cellulae basales ad 60  $\mu\text{m}$  latae, cellulae mediae ad 35  $\mu\text{m}$  latae, cellulae apicales minus quam 10  $\mu\text{m}$  latae), recta, glandulifera eglanduliferave; corollae mediae grandesve (20–35 mm longae), rosiae.

Leaf divisions mostly 3–5, occasionally 6–7 divided; pubescence moderate on stems and calyces, moderate to sparse on leaves; trichomes medium to long (5–12 cells), slender (basal cells up to 60  $\mu\text{m}$  wide, middle cells 35  $\mu\text{m}$  wide, apical cell less than 10  $\mu\text{m}$  wide), straight, glandular or eglandular; corollas 20–35 mm long, pink.

*Paratypes.* Orange Co., Hwy. 74, 13.4 mi E of junction with I-5, *Gordon and Gordon 766* (SFSU); Trabuco Canyon, *Holland 45* (MACF). Riverside Co., 8 mi NW of Elsinore, *Hitchcock 6041* (A, MO, NY, RSA, UC); near and above Banning on Idyllwild cutoff, *Gould 2142* (CAS, DS, GH, MO, UC, US). San Bernardino Co., Waterman Canyon, *Munz 2236* (DS, POM). San Diego Co., Richman Ranch, near DeLuz, *Gander 8194* (SD).

*Distribution.* Subsp. *leptotrichomum* occurs in chaparral in the Santa Ana, San Jacinto, and San Bernardino mts. In the Santa Ana Mts., the plants are found primarily in the region between Corona and San Juan Capistrano. In the San Jacinto Mts., they occur only on the northwestern slope from 610–762 m. In the San Bernardino Mts., they occur on the western slope, with larger stands in the vicinity of Lake Arrowhead.

This subspecies is most similar to subsp. *glandulosum* with respect to pubescence, but the trichomes are more slender and are consistently shorter with fewer cells than in subsp. *glandulosum*. In the San Jacinto and San Bernardino mts., pubescence density is variable; frequency of leaves with 6–7 divisions in the San Bernardino Mts. is intermediate between the Santa Ana Mt. population and subsp. *glandulosum* in the San Gabriel Mts. Plants in the San Jacinto Mts. often bear corolla limbs with apiculate lobes. Feb–Jul.

The Santa Ana Mt. population may represent a long-standing disjunction. There is no geographical evidence of any recent connection across the Los Angeles Basin with populations in the Santa Monica or San Gabriel mts., based on herbarium collections. Although high levels of compatibility occur between subsp. *leptotrichomum* (pistillate parent) and subsp. *glandulosum* (85.7%), reduced levels of compatibility were noted in the reciprocal cross (63.6%).

San Jacinto and San Bernardino mt. populations constitute geographically isolated entities. With respect to trichome type, however, both populations appear to be intermediate between Santa Ana and San Gabriel mt. populations. In both cases, trichomes vary from



those that resemble subsp. *leptotrichomum* to those that possess a mixture of both trichome types on one plant. Trichome thickness, glandularity, density, and leaf lobe number never reach the extreme of subsp. *glandulosum*, and are often nearly indistinguishable from *leptotrichomum*. Therefore, plants in the San Jacinto and San Bernardino mts. are included in subsp. *leptotrichomum*.

4. *Leptodactylon californicum* Hook. & Arn., Bot. Beechey's Voy. 369. 1839. subsp. *californicum*.—*Gilia californica* Benth., A. D.C. Prod. 9:316. 1845.—*Navarretia californica* Kuntze, Rev. Gen. Pl. 2:433. 1891.—TYPE: Nova California, 1833, *Douglas s.n.* (holotype, LE, photo, CAS!).

Leaf divisions 3–5; pubescence moderate to dense on stems, moderate to sparse on calyces, and leaves glabrous; trichomes long, slender, wavy, predominantly eglandular; corollas generally small, 21–34 mm long, pink.

*Distribution.* Subsp. *californicum* occurs in the San Rafael, Santa Ynez, Santa Susana, and Santa Monica mts., and in scattered locations in Ventura County. A population occurs at the head of the Cuyama Valley, and a few specimens have been collected in the southern end of the La Panza, Santa Lucia, and San Luis ranges of San Luis Obispo Co. This subspecies occurs generally in chaparral or coastal sage scrub, and is found from near sea level (Santa Monica Mts.) to 610 m on Figueroa Mt. (San Rafael Mts.) on sandstone cliffs or roadcuts.

The combination of tomentosely pubescent stems and calyces, and glabrous leaves on plants of this subspecies is highly distinctive. Although corollas range from 21–34 mm long ( $\bar{x}$  = 26.96, SD = 2.75), they are generally smaller than in other areas of the species range, and often pale pink. Jan–Jun (late Dec in the Santa Susana Mts.).

5. *Leptodactylon californicum* Hook. & Arn. subsp. **tomentosum** Gordon subsp. nov.—TYPE: USA, California, San Luis Obispo Co., Dunes near Oso Flaco Lake, 20 Apr 1981, *Gordon 823* (holotype, CAS; isotypes, LA, OBI, RSA, UC, UCSB, US).

Folia 3–5 divisio; caulis et calycis indumentum dense tomentosae, foliorum moderatum sparsumve; trichomata longa, gracilia, plerumque eglandulifera; corollae 19.6–30.5 mm longae, rosiae; corollarum tubi 1.4–2.4 mm lati.

Leaf divisions 3–5; stems and calyces densely tomentosely pubescent; leaf pubescence sparse to moderate; trichomes long, slender, largely eglandular; corollas 19.6–30.5 mm long, pink; corolla tubes wide, 1.4–2.4 mm.



*Paratypes.* San Luis Obispo Co., Oso Flaco Lake, end of Oso Flaco Road, dunes N of road, *Gordon 823* (CAS, LA, OBI, RSA, SFSU, UC, UCSB, US); Nipomo Mesa, *Mason 12402* (DS, MO, NY, PH, POM, UC). Santa Barbara Co., sand dunes N of Guadalupe, *Purser 7981* (SD).

*Distribution.* Subsp. *tomentosum* occurs in the coastal strand region of San Luis Obispo and Santa Barbara counties. Based on herbarium records, it appears that plants were once common from Pismo Beach to Oso Flaco Lake, but at present they are largely restricted to the vicinity of Oso Flaco Lake and Nipomo Mesa (Gordon 1983). Plants occur both on front dunes and on older, more stabilized back dunes. Plants on front dunes appear shorter and more compact than those on back dunes.

Pubescence resembles that of subsp. *californicum*, but is much denser, overall, and often extends onto leaves. Corolla tubes are significantly wider in this group (subsp. *tomentosum*:  $\bar{x}$  = 1.94 mm; all other subspecies:  $\bar{x}$  = 1.53–1.72 mm). Internodes are always short, resulting in crowded leaves that add to the “dense” aspect of these plants. Mar–Aug.

The coastal strand population resembles subsp. *californicum* and the geographical distance between these two groups is not great. This population is recognizably distinct, though, due to its markedly denser pubescence, particularly on leaves. This distinction was also noted by Hoover (1970). A certain amount of isolation, in conjunction with the particular environmental conditions of this habitat, may be responsible for these differences (Gordon 1983).

#### ACKNOWLEDGMENTS

This paper is the result of a master's thesis submitted to the Department of Biological Sciences, San Francisco State University. I thank Drs. Stan Williams and Barry Tanowitz for reviewing earlier versions of this manuscript, Dr. Dale Smith for his review and insightful comments relative to the Polemoniaceae, and reviewers Dr. Dieter Wilken, Joanna Tomassacci, and Dr. David Keil for their helpful suggestions. I particularly thank Dr. R. W. Patterson for preparation of Latin descriptions, many enlightening discussions, and continued encouragement. Thanks to Doug Shields and Vicki Cypherd (ERCE) for assistance with graphics. Appreciation is extended to curators of the following herbaria for access to their specimens: SD, IRVC, RSA, UCR, OBI, LA, MACF, NY, PH, US, GH, A, MO, and POM.

#### LITERATURE CITED

- ABRAMS, L. R. 1910. A phytogeographic and taxonomic study of the southern California trees and shrubs. *Bull. New York Bot. Gard.* 6:438.  
BENTHAM, G. 1845. Polemoniaceae. *In* A. D.C. *Prodromus*, 9:316.  
EASTWOOD, A. 1904. Some new species of western Polemoniaceae. *Bot. Gaz. (Crawfordsville)* 37:437–447.  
GORDON, P. 1983. A biosystematic investigation of variation in the *Leptodactylon californicum* complex. M.A. thesis. San Francisco State Univ., San Francisco.



- GRANT, V. 1959. Natural history of the *Phlox* family: systematic botany. M. Nijhoff, The Hague.
- HOLLAND, R. F. 1986. Preliminary descriptions of the terrestrial natural communities of California. State of California, The Resources Agency, Department of Fish and Game, Sacramento.
- HOOKE, J. D. and G. A. W. ARNOTT. 1839. Bot. Beechey's Voy. pt. 8:369, pl. 89.
- HOOVER, R. F. 1970. The vascular plants of San Luis Obispo County, California. Univ. California Press, Berkeley.
- KUNTZE, O. 1891. Polemoniaceae. *Revisio generum plantarum* 2:432–434.
- MASON, H. L. 1951. Polemoniaceae. Pp. 396–474 in L. R. Abrams, *Illustrated flora of the Pacific states*, Vol. 3. Stanford Univ. Press, Stanford, CA.
- MUNZ, P. A. 1959. A California flora. Univ. California Press, Berkeley.
- PATTERSON, R. 1977. A revision of *LINANTHUS* sect. *SIPHONELLA* (Polemoniaceae). *Madroño* 24:36–48.
- STEBBINS, G. L. 1950. Variation and evolution in plants. Columbia Univ. Press, New York.
- . 1974. Flowering plants: evolution above the species level. Belknap Press of Harvard Univ. Press, Cambridge.
- TIMBROOK, S. 1986. Segregation of *Loeseliastrum* from *Langloisia* (Polemoniaceae). *Madroño* 33:157–174.
- WHERRY, E. T. 1945. Two linanthoid genera. *Amer. Midl. Naturalist* 34:381–387.
- ZAR, J. H. 1974. Biostatistical analysis. Prentice-Hall, Inc., Englewood Cliffs, NJ.

(Resubmitted 23 Nov 1988; revision accepted 20 Sep 1989.)

## ANNOUNCEMENT

### NEW PUBLICATION

LITTLE, ELBERT L. JR. and ROGER G. SKOLMEN. 1989. *Common forest trees of Hawaii*. v + 321 pp. 8 maps, 152 line drawings, 12 color plates. Agriculture Handbook no. 679, U.S.D.A. Forest Service.—An illustrated reference for identifying 152 common trees in forests of Hawaii, of which 60 are native (53 endemic), 7 introduced by early Hawaiians, and 85 introduced since first contact by Europeans. The book has a general introduction, lists of special areas, champion trees, weed trees, and poisonous trees, and a discussion of forests and forestry in Hawaii. Maps include distribution of forest types and forest reserves of each island. Trees are grouped by family in systematic order; each species is listed by both common name and scientific name. For each there is a semitechnical description, a discussion of wood characteristics and economic value, distribution and habitat within the state, special areas where the tree may be found, dimensions of champion trees, overall range, and other common names. The book has a selected bibliography and an index to common names, scientific names, and families.—\$16.00 (in paperback), also available in hardcover (price unknown). For sale by Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402. Stock no. 001-000-04536-9.



A SYSTEMATIC AND BIOGEOGRAPHIC REVIEW OF  
*RAILLARDIOPSIS* [*RAILLARDELLA*] *MUIRII*  
(ASTERACEAE: MADIINAE), WITH SPECIAL  
REFERENCE TO A DISJUNCT CALIFORNIA  
COAST RANGE POPULATION

BRUCE G. BALDWIN and DONALD W. KYHOS  
Department of Botany, University of California,  
Davis, CA 95616

ABSTRACT

Morphological, cytological, and controlled growth chamber studies demonstrate that a widely disjunct *Raillardiopsis* population in the Santa Lucia Range of central coastal California is conspecific with *R. [Raillardella] muirii* of the southern Sierra Nevada. Morphological and cytological variation detected within Sierran *R. muirii* essentially encompasses that of the Santa Lucia Range population. A revised description of this little understood species and a key to the two species comprising the genus are presented. Biological and geological considerations bearing on the origin of the Santa Lucia Range disjunction are discussed. High dispersibility, paleoecological factors, and plate tectonics have potentially contributed to this seemingly enigmatic species distribution.

The isolated occurrence of a *Raillardiopsis* population on Ventana Double Cone in the Santa Lucia Mountains of central coastal California has been regarded “. . . a phyto-geographic occurrence of first magnitude in California floristics” (Howitt and Howell 1973). This population indeed raises interesting questions about the evolutionary history of *Raillardiopsis*, a little-known genus resurrected from within *Raillardella* based on morphological, cytological, and chloroplast DNA evidence (Baldwin 1989). The two rare species comprising *Raillardiopsis* have ranges far removed from the Santa Lucia Mountains. *Raillardiopsis scabrida* (Eastw.) Rydb. is restricted to high peaks and ridges in the inner North Coast Ranges of California from Lake to Trinity counties, with two Southern Cascade outliers in Shasta County. *Raillardiopsis muirii* (A. Gray) Rydb. (Figs. 1 and 2) has long been considered a southern Sierra Nevada endemic. In a group of rare perennials a disjunction of the magnitude represented by the Santa Lucia Range population could have important systematic or biogeographic implications.

Though the existence of the Ventana Double Cone population has been known since 1962, when it was discovered by Clare Hardham (Griffin 1975), the specific identity of these plants has remained ambiguous. This is largely attributable to lack of specimens from this remote locality and inadequate published descriptions of *Raillardiopsis* species. The earliest reference to the Santa Lucia plants



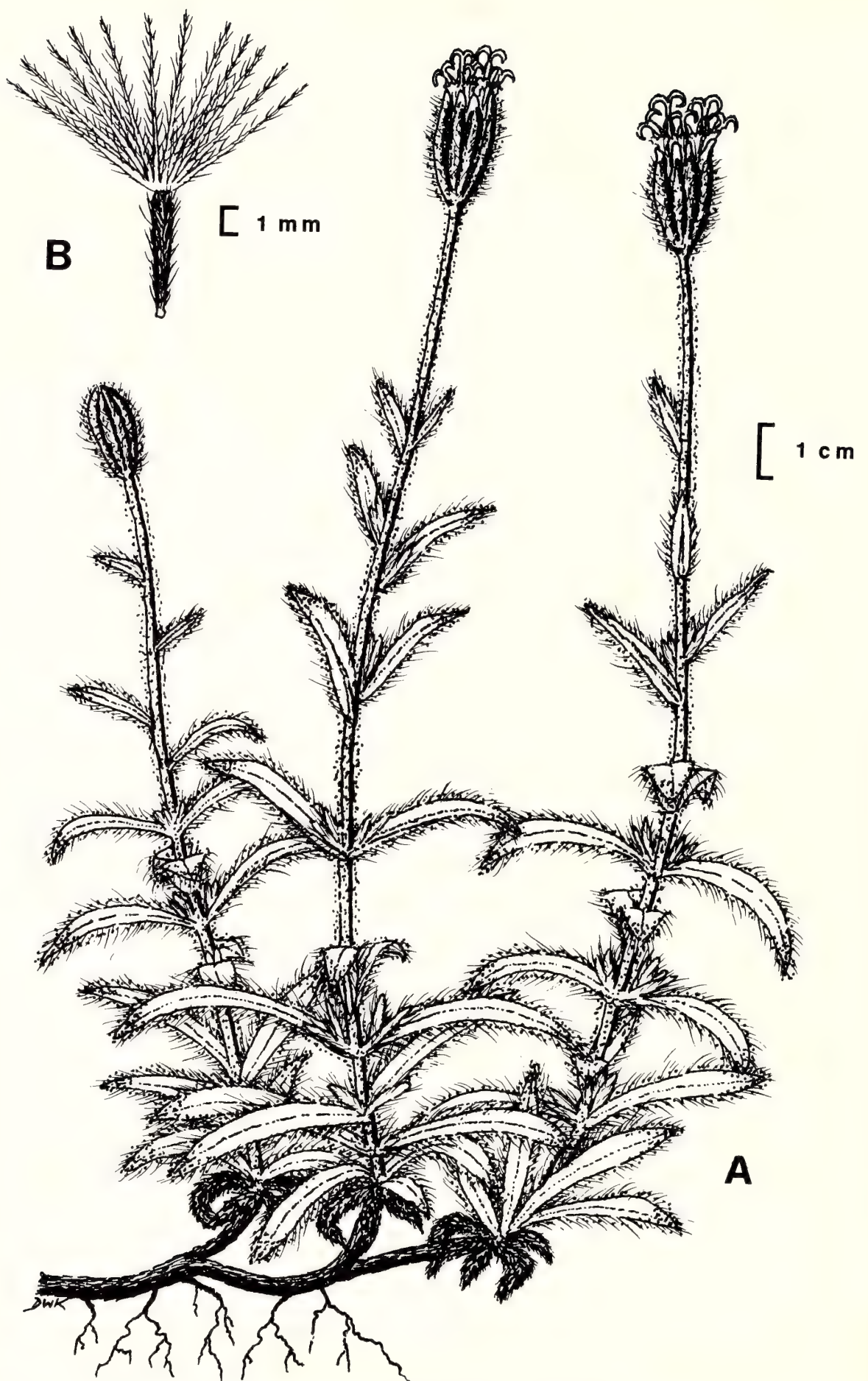


FIG. 1. *Raillardiopsis muirii* (A. Gray) Rydb. A. Habit. B. Mature achene with pappus.





FIG. 2. Capitulum of *Raillardiopsis muirii*. Note the distinctive spreading trichomes on the abaxial bract surfaces.

as *Raillardiopsis* (Howitt and Howell 1973) immediately followed the first known collection made in 1972 [*Steven Talley s.n.* (DAV)]. Further study by J. R. Griffin revealed that the Ventana plants shared closest relationship, and were perhaps conspecific, with *R. muirii*. Griffin (1975) concluded, "if the Ventana population is *R. muirii*, this plant is one of the most restricted and most interesting montane disjuncts in the Santa Lucias; if it is a new species, it is probably the most restricted endemic above 1200 m". Unfortunately, further work was hindered following the Marble Cone Fire of 1977 because of trail closure and shrub overgrowth.

This study was undertaken to assess the evolutionary and biogeographic relationships of the Santa Lucia Range (hereafter "Ventana") *Raillardiopsis* to *R. muirii*. Morphological, cytological, and reproductive characteristics of these plants were investigated. An improved description of *R. muirii* and a key differentiating this species from the similar *R. scabrida* were prepared to prevent future confusion concerning the limits of these taxa.



## FIELD OBSERVATIONS

The first author visited Ventana Double Cone in July of 1986 and found a vigorous *Raillardiopsis* population on the steep western slope. The plants were scattered mats in decomposing granitic scree and bedrock crevices with little other vegetative cover. A few small plants were previously observed on and immediately east of the summit in 1975 and 1981 (V. Yadon oral comm.). The similar granitic slopes of "Ventana"—the notched ridge north of Ventana Double Cone—and on Ventana Cone may support additional *Raillardiopsis* populations.

## METHODS

Vouchers, floral buds, and achenes were field-collected. Buds were fixed in Carnoy's (6 ethanol : 3 chloroform : 1 glacial acetic acid; v:v:v) or modified Carnoy's (6 chloroform : 3 ethanol : 1 glacial acetic acid) solutions. Chromosome counts and meiotic associations were determined at meiotic metaphase I in acetocarmine. Pollen fertility was estimated from percent stainability with cotton blue in lactophenol. Fourteen Ventana [*Baldwin 618* (DAV)], six *R. muirii* [*Baldwin 683* (DAV)], three  $F_1$  *B618* (seed)  $\times$  *B683* (pollen), and nine  $F_1$  *B683* (seed)  $\times$  *B618* (pollen) plants were grown from seedlings under uniform growth chamber conditions (21°C, 16 hour light; 11°C, 8 hour dark) in U.C. potting mix or with ca. equal amounts of coarse pumice. Artificial hybridizations were performed by rubbing pollen-shedding capitula together. These hybridizations involved the same Ventana parent but different *R. muirii* individuals. Embryos were excised and germinated under continuous light. Parental embryos were germinated on wet filter paper. After surface-sterilization (10% bleach, 20 min),  $F_1$  embryos were excised and germinated on Murishige minimal organics media (GIBCO 510-3118) + 2% sucrose. Self-incompatibility of Ventana *Raillardiopsis* was assessed by identifying all progeny from interspecific crosses with species other than *R. muirii* serving as staminate parents. Additionally, fruit set in all unmanipulated heads was monitored. Herbarium specimens at CAS, CHSC, DAV, GH, JEPS, PGM, RSA, THRI, and UC were examined. These represented 12 of the 18 known populations of *R. muirii*, several populations of *R. scabrida*, and all known collections of Ventana *Raillardiopsis* (see Baldwin 1989).

## RESULTS AND DISCUSSION

*Morphological comparisons.* The range of morphological variation detected in *R. muirii* essentially encompassed that found in the Ventana population. The only exceptions were slightly greater leaf crisping, leaf deflexion, and leaf width among some Ventana indi-



viduals relative to any *R. muirii* examined. These differences persisted under growth chamber conditions in individuals grown from seedlings. *Raillardiopsis muirii* displayed no crisping under these conditions, though this character was observed to a minor degree in field material. Artificial hybridization between Ventana and *R. muirii* individuals also indicated a genetic basis for leaf crisping in Ventana plants. All but two individuals of the  $F_1$  generation displayed noticeable leaf crisping, regardless of the population serving as seed parent. All other (interspecific) combinations involving Ventana *Raillardiopsis* (Baldwin 1989) have yielded  $F_1$  individuals with evident leaf crisping.

*Cytology.* Chromosome counts of all *R. muirii* (B615, B653, B683) and Ventana *Raillardiopsis* (B618) revealed eight bivalents at meiotic metaphase I. The single report of  $n=16$  for *R. muirii* (Powell and Powell 1978) is a miscommunication of a somatic count ( $2n=16$ ) by Kyhos et al. (Carlquist 1959). Pollen stainabilities of single Ventana (99%; B618) and *R. muirii* (84%; B683) plants indicated normal fertility. Meiotic analyses of the *R. muirii*  $\times$  Ventana  $F_1$  generation revealed a modal configuration of six bivalents and a ring of four in five individuals, and consistently eight bivalents in three plants. Unambiguous hybrid morphology (leaf crisping) in one of the latter three plants, of Sierran seed-parentage, strongly suggests chromosomal structural heterozygosity in the parental *R. muirii* population, i.e., one genome being shared with the Ventana population, the other differing by a single reciprocal translocation. Pollen fertility ranged from 35% to 50% ( $\bar{x} = 43.6\%$ ) in the structurally heterozygous  $F_1$  plants and from 56% to 66% ( $\bar{x} = 60.3\%$ ) in the structurally uniform  $F_1$  individuals. *Raillardiopsis muirii*  $\times$  Ventana hybrids were easily produced in both directions. The chromosomal divergence detected within *R. muirii* is minor compared to that found between *R. muirii* and *R. scabrida* (Baldwin 1989). All chromosome counts of *R. scabrida* [Baldwin 620 (DAV), Baldwin 676 (DAV), Taylor et al. 9089 (DAV, RSA)] have revealed  $n=7$ , in agreement with counts by Strother (1983).

*Breeding system.* Ventana *Raillardiopsis* is strongly self-incompatible. Reportedly, interspecific crosses in Madiinae can elicit selfing in otherwise self-incompatible species (Clausen et al. 1945). All but one progeny from 104 Ventana *Raillardiopsis* heads utilized as pistillate parents in crosses with Madiinae other than *R. muirii* were, however, hybrid or inviable. The single plant resulting from selfing was unusually robust and morphologically distinctive, with corolla, bract, and habit aberrations. No unmanipulated heads bore fruit.

*Taxonomic conclusions.* Comparative evidence indicates that the Ventana *Raillardiopsis* population belongs within *R. muirii*. We hesitate to segregate the Ventana element as a subspecies given its lack



of sharp morphological distinction from all Sierran populations. Subspecific recognition of these plants would require reliance on small modal differences as diagnostic morphological characters, not allowing definite identification of specimens from unknown localities. Apparent morphological variation among Sierran populations indicates that such treatment would necessitate further dissection of the species into taxa of questionable phylogenetic significance.

*Revised description.* Confusion about the identity of the Ventana population was, in part, attributable to descriptions of *R. muirii* from few and fragmentary herbarium records. This situation has improved, largely owing to J. T. Howell (see Howell 1961), L. Norris, and J. Shevock, who extensively collected *R. muirii* in the southern Sierra Nevada. The following description and key to *Raillardiopsis* are provided to clarify *R. muirii* and to allow identification of any populations that may await discovery.

**RAILLARDIOPSIS MUIRII** (A. Gray) Rydb., North American Flora 34: 318–320. 1927 (Fig. 1). — *Raillardella muirii* A. Gray, Bot. Calif. 1:618. 1876. — TYPE: USA, California, Sierra Nevada, “the station unknown”, *J. Muir s.n.* (holotype, GH!; isotype, CAS!). According to a letter accompanying the holotype from John H. Redfield to Asa Gray (28 Feb 1876), the type specimen was “. . . in a small collection sent . . . by John Muir—from the Sierras in vicinity of Yosemite”. No other collection information was given. The most northerly populations known are in the Kings River drainage. Muir’s earliest explorations of the Kings River region occurred in 1873 and 1875, including the North Fork of the Kings River vicinity and the “yosemite of the Middle Fork of the King’s River”—Tehipite Valley (Muir 1938, 1977). These two areas possess the largest and most extensive known *R. muirii* populations (CNDDDB 1989). The species was rediscovered by Alice Eastwood in 1905 at Tehipite Valley (Eastwood 1907).

Clumped to mat-forming herbaceous perennial with spreading, often extensively branched, woody rhizomes, to at least 1.5 cm diam. Aerial stems several to many, crowded, the short, densely-leaved vegetative shoots and dead growth often forming carpets extending to at least 2.25 m. Flowering stems erect to ascending, leafy throughout, 7–54 cm high, simple to several branched, generally from above middle, greenish-yellow to dark purplish, white-hirsute to villous and sparingly glandular below, the hispidulous, spherical to tack-shaped gland-tipped hairs becoming predominant above. Leaves green to gray-green, sessile, linear to narrowly lanceolate, entire, flat to strongly crisped-coiled, ascending to apically or basally deflexed, 9–42 mm long, (1–)2–5(–6) mm wide, to smaller at extreme base of stem and above lowest branches or axillary shoots, opposite at base



to above middle, alternate above, irregularly white-hirsute to villous and glandular; glands like those on stems, most conspicuous on leaf apices and upper leaves; leaf apices abruptly to narrowly acute; leaf margins slightly revolute. Heads terminating stems and branches, discoid, (elliptic-) narrowly to broadly campanulate or turbinate; capitular bracts green to purple, 8–13 mm high, (5–)7–16, uniseriate, subequal, mostly half-enveloping single florets with fewer, nearly paleaceous bracts between these, basal margins largely coalescent at anthesis, to mostly free and spreading at fruiting maturity, white-hirsute to villous and conspicuously glandular abaxially and on inner apex, with prominent, stramineous, essentially glabrous adaxial midrib; florets 7–29, all functionally bisexual; corollas yellow, 6.5–10 mm long, tubular, constricted basally; anthers yellow; stylar branches hispidulous. Achenes black, 4–7.5 mm long, 0.5–1.2 mm wide, terete, linear, straight to slightly curved at acute base, densely white ascending-hirsute; pappus bristles flattened, ciliate-plumose to tip, purplish-white to tawny, 9–17, 5–11 mm maximum length. Chromosome number  $n=8$ .

Under growth chamber conditions certain characters exceeded the above. Main stem leaves of one Ventana individual became very robust, to 9 mm wide. Unusually extensive branching of most plants was also observed.

KEY TO SPECIES OF *RAILLARDIOPSIS*

- A. Heads strictly discoid; bracts hirsute to villous and glandular abaxially; achenes 4–7.5 mm long, 0.5–1.2 mm wide; pappus length equal to or longer than achene; leaves green to grayish-green, markedly acute, not auriculate-clasping on upper stem. .... *R. muirii*
- A' Heads with 0–3 rays; bracts glandular abaxially with villous apical margins; achenes 5–9 mm long, 1.3–2.4 mm wide; pappus length equal to or shorter than achene; leaves blue-green to grayish blue-green, acute to obtuse, often auriculate-clasping on upper stem. .... *R. scabrida*

Heads of live, rayless *R. scabrida* often appear distinctly elliptic in silhouette, or constricted at summit of bracts, to a much greater extent than those of *R. muirii*. This character is obscured in pressed material.

*Distribution and ecology.* *Raillardiopsis muirii* is a California endemic known from ca. 19 populations (Fig. 3) on granitic exposures or granitic-derived soils in mixed conifer forest and chaparral openings, mountain slopes, ridges, and valley bottoms from 1190 to 2500 m elevation in the southern Sierra Nevada from Fresno to Kern counties and on Ventana Double Cone, Santa Lucia Range, Monterey County (CNDDDB 1989). With the exception of three southern outliers (Baker Point, Church Dome, Owens Peak), the Sierra Nevada populations are confined to the drainages of the Kings River and Kaweah River. Flowering has been reported from early June to



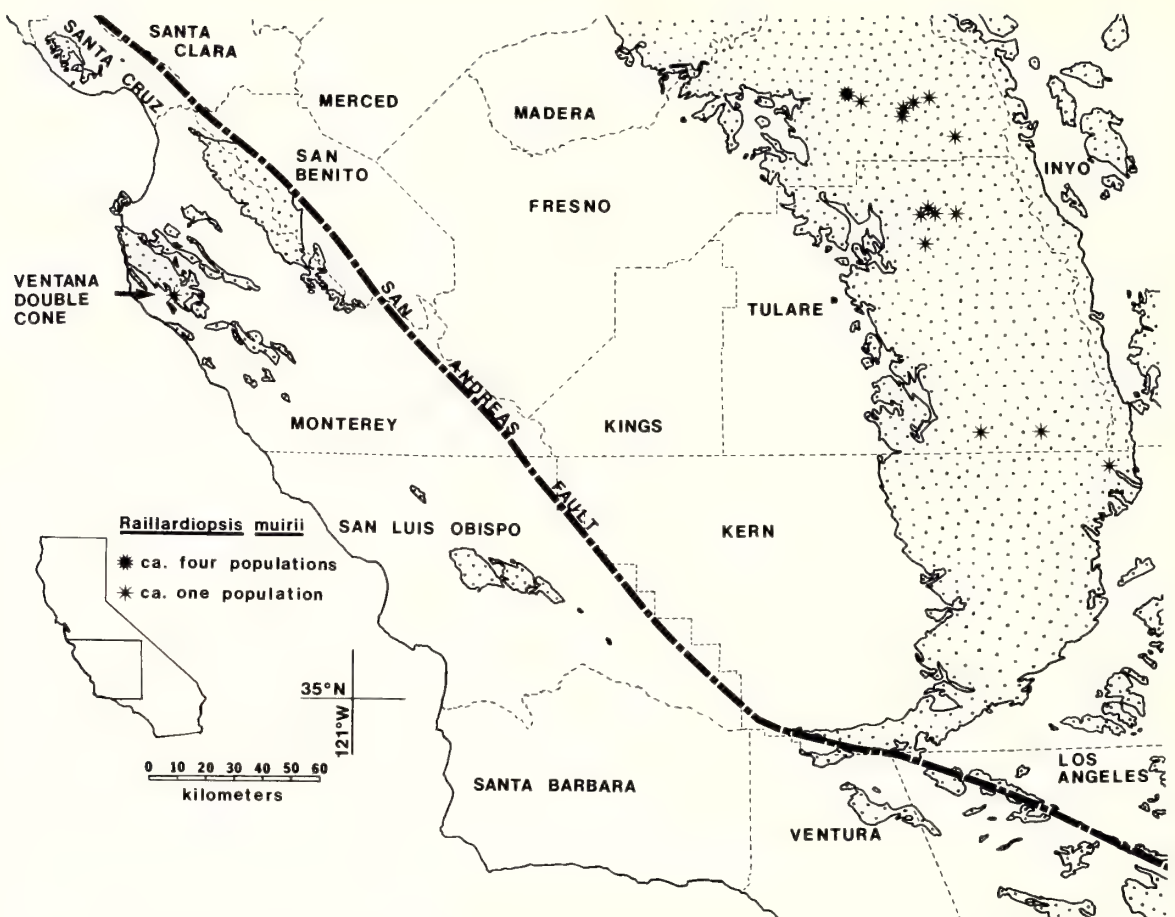


FIG. 3. Natural distribution of *Raillardiopsis muirii* and granitic exposures (stippled areas) in central California. Extensive non-granitics within the Sierran batholith are not shown.

early October, one collection nearing anthesis in mid-May. Several populations are reported to comprise fewer than 100 individuals (CNDDDB 1989). The species is listed as “rare and endangered” by the California Native Plant Society (Smith and Berg 1988) and as a “sensitive” species by the U.S. Forest Service (J. Shevock pers. comm.).

*Biogeographic history.* The major range disjunction between Sierran and Ventana *R. muirii* populations is remarkable in light of their apparent restriction to granitic substrates (Fig. 3). Granitic exposures in the South Coast Ranges of California are limited and widely separated because of extensive blanketing of the Salinian pluton basement by late Cretaceous and Cenozoic sediments (Page 1966, 1981, 1989; Compton 1966). The youngest significant overlying sediments reported to contact basement are Miocene, when the Santa Lucia Range was submarine (Raven and Axelrod 1978). Given the Oligocene age of the oldest Compositae fossil evidence (Muller 1981), it appears that granitic exposure in the South Coast Ranges has not exceeded its present extent within the history of *R. muirii*.

*Raillardiopsis muirii* may have had a wider ecological amplitude in the past. The species has no mineralogical requirement for granitic



soils, based on successful cultivation in non-granitic mixes. Mortality from root necrosis and microbial infection was, however, encountered and may be a significant factor in the field. Present occurrence in sites with little plant cover may reflect secondary restriction to habitats with reduced competitive interference, as proposed for "paleoendemic" or ecotype "depleted" taxa (Stebbins 1942; Raven and Axelrod 1978). *Raillardiopsis scabrida* occurs in similarly semibarren sites on Franciscan metamorphic substrates. The patchy distribution of both species and their large geographic separation from one another suggest more extensive past occurrence. Fossil evidence demonstrates that many narrowly-endemic taxa in California were once considerably more widespread (Raven and Axelrod 1978).

The presence of relict *Abies bracteata* in the Santa Lucia Range indicates that these mountains have served as a refugium. This species, known from fossil Miocene floras in western Nevada (Axelrod 1976), is today restricted to the Santa Lucia Range, including Ventana Double Cone. Axelrod suggested that *A. bracteata* probably occurred in the Sierra Nevada during the Pliocene, and perhaps in the more southerly Coast Ranges, until the Xerothermic Period of the Quaternary, but was eliminated in both regions by the drier, warmer climate. These xerothermic conditions would likely have had similar impact on any populations of *R. muirii* bridging the Santa Lucia Range and southern Sierra Nevada.

Modern associates of both Sierran and Ventana *R. muirii* offer little to argue for past continuity of similar plant communities. *Raillardiopsis muirii* occurs in a variety of Sierran vegetation types, most of the reported associated species having wide distributions. Several perennial species intimately co-occurring with at least one Sierran *R. muirii* population are found on Ventana Double Cone, including *Dudleya cymosa*, *Eriogonum nudum*, *E. saxatile*, *Garrya flavescens*, *Penstemon breviflorus*, *Pellaea mucronata*, *Pinus ponderosa*, *Polystichum munitum*, *Potentilla glandulosa*, *Pteridium aquilinum*, *Quercus chrysolepsis*, and *Q. kelloggii*. Close Sierran associates found on other high granitic peaks in the Santa Lucia Mountains include *Brickellia californica* and *Pinus lambertiana* (CNDDDB 1989; Griffin 1975; Howell 1961). None of these species is as geographically restricted as *R. muirii* (Munz 1959). *Pinus lambertiana* and several additional taxa discussed by Griffin (1975; e.g., *Allium burlewii*, *A. campanulatum*, *Carex multicaulis*, *Chimaphila menziesii*, *Cornus nuttallii*, *Ribes roezlii*, *Sanicula graveolens*) are, however, Santa Lucia Range montane disjuncts that also occur in the southern Sierra Nevada.

Establishment of an *R. muirii* population by long-distance dispersal between the Sierra Nevada and Santa Lucia Range is problematic. The minimum distance between Ventana Double Cone and



the closest Sierran population is ca. 240 km. Strong self-incompatibility would have necessitated the eventual establishment of at least two individuals bearing different S-alleles.

Nonetheless, a dramatic example of such dispersal is known in Madiinae. Dispersal between the Sierra Nevada and Santa Lucia Range pales by comparison to the migration event necessary to account for Hawaiian Madiinae (Baldwin 1989). Given the widespread occurrence of self-incompatibility among Hawaiian tarweeds, it appears that the founding colonist(s), in addition to traveling over 3500 km from North America, had to contend with an initial shortage of S-alleles (Carr et al. 1986). This comparison has special relevance for three reasons: (1) chloroplast DNA and biosystematic evidence indicate that *R. muirii* is among the closest extant relatives of Hawaiian Madiinae (Baldwin 1989); (2) propagule characteristics of *R. muirii* are similar to Hawaiian Madiinae species that have undergone repeated inter-island dispersal (e.g., *Dubautia plantaginea*; Carr 1985); and (3) the rhizomatous habit of *R. muirii* would seemingly permit indefinite clonal propagation, allowing persistence of a single self-incompatible colonist while accumulating the S-allele mutations necessary for renewed sexual reproduction, as postulated by Carr et al. (1986) for origin of Hawaiian Madiinae.

Plate tectonics suggests an intriguing hypothesis to explain the Ventana disjunction without long-distance dispersal or wider ecological occurrence of *R. muirii* in prehistoric time. Earliest exposure of granitics in the Gabilan and northern Santa Lucia Ranges after the Miocene could have occurred as long as five million years ago (Stephan A. Graham, Stanford Univ., oral comm.). The Santa Lucia Range was then ca. 240 km southeasterly, based on 48 mm of average annual northwesterly slip of the Salinian Block along the San Andreas Fault (Fig. 3; DeMets et al. 1987). This placed the Tehachapi/San Emigdio granitics, continuous with those of the southern Sierra Nevada, in juxtaposition with the Gabilan Range. The extensive Gabilan granitics are today only 15 km from Santa Lucia exposures nearly continuous with those of Ventana Double Cone (Jennings and Strand 1958). Uplift estimates (Huber 1981) suggest that Sierran granitic exposure was extensive by late Miocene. A wider early Pliocene distribution of *R. muirii* along the southern Sierran Batholith into the San Emigdio region is therefore conceivable. Any populations then extending onto Gabilan or Santa Lucian granitics could have been transported in situ 240 km northwesterly by tectonic slippage along the San Andreas Fault.

Such displacement of *R. muirii* would require that this species is at least five million years old. Though no fossil evidence of Madiinae has been reported, extant tarweed genera are thought by Raven and Axelrod (1978) to have occurred within California by the Pliocene. Accordingly, DNA phylogenetic evidence demonstrated divergence



of *R. muirii* and *R. scabrida* prior to the origin of Hawaiian Madiinae (Baldwin 1989). Hawaiian Madiinae appear to be of Kauaian or pre-Kauaian origin (Carr et al. 1989). *Raillardiopsis muirii* is, therefore, conceivably greater than six million years old.

In conclusion, geological and biological considerations reveal that the distribution of *R. muirii* is far from inexplicable. Multiple tenable hypotheses could explain the natural occurrence of *R. muirii* on Ventana Double Cone. Considerable chloroplast DNA differentiation between this population and one from the Sierra Nevada (Baldwin 1989) offers hope for further biogeographic clarification within this species.

#### ACKNOWLEDGMENTS

We thank D. Axelrod, G. Carr, J. Griffin, A. Juncosa, D. Keil, J. Shevock, and J. Strother for helpful reviews and discussion; S. Bainbridge and B. Cassidy for field assistance; R. Palmer for *Raillardiopsis scabrida* from Shasta County; G. Carr for cytological assistance; and the curators of the cited herbaria for loans or access to specimens.

#### LITERATURE CITED

- AXELROD, D. I. 1976. Evolution of the Santa Lucia fir *Abies bracteata* ecosystem. *Ann. Missouri Bot. Gard.* 63:24–41.
- BALDWIN, B. G. 1989. Chloroplast DNA phylogenetics and biosystematic studies in Madiinae (Asteraceae). Ph.D. dissertation. Univ. California, Davis.
- CALIFORNIA NATURAL DIVERSITY DATA BASE. 1989. Data file. Calif. Dept. Fish and Game, Sacramento.
- CARLQUIST, S. 1959. Studies on Madiinae: anatomy, cytology, and evolutionary relationships. *Aliso* 4:171–236.
- CARR, G. D. 1985. Monograph of the Hawaiian Madiinae (Asteraceae): *Argyroxiphium*, *Dubautia*, and *Wilkesia*. *Allertonia* 4:1–123.
- , E. A. POWELL, and D. W. KYHOS. 1986. Self-incompatibility in the Hawaiian Madiinae (Compositae): an exception to Baker's Rule. *Evolution* 40:430–434.
- , R. ROBICHAUX, M. S. WITTER, and D. W. KYHOS. 1989. Adaptive radiation of the Hawaiian silversword alliance (Compositae–Madiinae): a comparison with the Hawaiian picture-winged *Drosophila*. Pp. 79–97 in L. V. Giddings, K. Y. Kaneshiro, and W. W. Anderson (eds.), *Genetics, speciation, and the founder principle*. Oxford Univ. Press, New York.
- CLAUSEN, J., D. D. KECK, and W. M. HIESEY. 1945. Experimental studies on the nature of species; II. Plant evolution through amphiploidy and autopolyploidy with examples from the Madiinae. Carnegie Institution of Washington Publ. No. 564, Washington, DC.
- COMPTON, R. R. 1966. Granitic and metamorphic rocks of the Salinian Block, California Coast Ranges. Pp. 277–287 in E. H. Bailey (ed.), *Geology of northern California*. Bulletin Calif. Div. Mines and Geology, San Francisco.
- DEMETS, C., R. G. GORDON, S. STEIN, and D. F. ARGUS. 1987. A revised estimate of Pacific–North America motion and implications for western North America plate boundary zone tectonics. *Geophys. Res. Lett.* 14:911–914.
- EASTWOOD, A. 1907. (Untitled note.) *Muhlenbergia* 3:78.
- GRIFFIN, J. R. 1975. Plants of the highest Santa Lucia and Diablo range peaks, California. USDA Forest Serv. Res. Paper PSW-110, Pacific Southwest Forest and Range Exp. Stn., Berkeley, CA.



- HOWELL, J. T. 1961. The Tompkins-Tehipite Expedition of the California Academy of Sciences. *Leafl. W. Bot.* 9:181-196.
- HOWITT, B. F. and J. T. HOWELL. 1973. Supplement to the vascular plants of Monterey County, California. Pacific Grove Press, Pacific Grove, CA.
- HUBER, N. K. 1981. Amount and timing of late Cenozoic uplift and tilt of the central Sierra Nevada, California—evidence from the upper San Joaquin River basin. *U.S. Geol. Survey Prof. Paper* 1197:1-28.
- JENNINGS, C. W. and R. G. STRAND. 1958. Geologic map of California, Santa Cruz sheet, O. P. Jenkins edition. Calif. Div. of Mines, San Francisco.
- MUIR, J. 1938. John of the mountains; the unpublished journals of John Muir. L. M. Wolfe (ed.). Houghton Mifflin, Boston.
- . 1977. Rambles in King's River country. L. Osborne, Ashland, OR.
- MULLER, J. 1981. Fossil pollen records of extant angiosperms. *Bot. Rev.* 47:1-142.
- MUNZ, P. A. 1959. A California flora. Univ. California Press, Berkeley.
- PAGE, B. M. 1966. Geology of the Coast Ranges of California. Pp. 255-276 in E. H. Bailey (ed.), *Geology of northern California*. Bulletin 190, Calif. Div. Mines and Geology, San Francisco.
- . 1981. The Southern Coast Ranges. Pp. 329-417 in W. G. Ernst (ed.), *The geotectonic development of California (Rubey; Volume I)*. Prentice-Hall, Englewood Cliffs, NJ.
- . 1989. The Salinian Block. Pp. 16-20 in C. Wahrhaftig and D. Sloan (eds.), *Geology of San Francisco and vicinity*. Field Trip Guidebook T105. Amer. Geophys. Union, Washington, DC.
- POWELL, A. M. and S. A. POWELL. 1978. Chromosome numbers in Asteraceae. *Madroño* 25:160-169.
- RAVEN, P. H. and D. I. AXELROD. 1978. Origin and relationships of the California flora. *Univ. of Calif. Publ. Bot.* 72:1-134.
- SMITH, J. P., JR. and K. BERG (eds.) 1988. Inventory of rare and endangered vascular plants of California. California Native Plant Society, Special Publication No. 1, 4th ed., Berkeley.
- STEBBINS, G. L. 1942. The genetic approach to problems of rare and endemic species. *Madroño* 6:241-258.
- STROTHER, J. L. 1983. More chromosome studies in Compositae. *Amer. J. Bot.* 70: 1217-1224.

(Received 6 Dec 1988; revision accepted 14 Nov 1989.)

## ANNOUNCEMENT

### SOUTHWESTERN BOTANICAL SYSTEMATICS SYMPOSIUM

The Sixth Annual Southwestern Botanical Systematics Symposium will be held May 25-26. This year's topic will be "Disjunctions and Their Significance." Invited speakers include: Mary T. Kalin Arroyo, Univ. of Chile; Daniel J. Crawford, Ohio State Univ.; Hong De-Yuan, Academia Sinica, People's Republic of China; David F. Murray, Univ. of Alaska; Clifford R. Parks and Margaret Hoey, Univ. of North Carolina; and Kenneth J. Sytsma, Univ. of Wisconsin. The evening address will be given by Charles B. Heiser, Jr., Univ. of Indiana. The cost is \$40.00 (\$30.00 for students), and includes Friday evening social, box lunch, and Saturday dinner. To register, send your name, address, and phone number, with a check payable to: Rancho Santa Ana Botanic Garden, Systematics Symposium, 1500 N. College Avenue, Claremont, California 91711. For more information, call (714) 625-8767.



*PUCCINELLIA HOWELLII* (POACEAE),  
A NEW SPECIES FROM CALIFORNIA

JERROLD I DAVIS

L. H. Bailey Hortorium, Cornell University,  
Ithaca, NY 14853

ABSTRACT

*Puccinellia howellii*, a new species from the Trinity Mountains of California, is described. As is typical of the genus, this species occurs in mineralized soils, in this case in a series of mineralized seeps; it is known only from the type locality. The new species is morphologically similar to *P. pumila*, a species of coastal habitats.

In April 1954, John Thomas Howell and Lewis S. Rose visited a mineralized seepage area in the Trinity Mountains, west of Whiskeytown, Shasta County, CA, and collected an unusual *Puccinellia*. Observing that plants from this site could not be assigned readily to any previously described species, Howell brought his collection to the attention of Jason Swallen, of the Smithsonian Institution (correspondence attached to Howell specimen at CAS). Swallen agreed that the plants were "curious," but neither he nor Howell subsequently described a new taxon. In the course of my studies of *Puccinellia*, I too have found the plants of the Whiskeytown population curious; they are distinct and warrant taxonomic recognition. In describing this species I honor the collector who first drew attention to its unique nature.

*Puccinellia howellii* Davis, sp. nov. (Fig. 1). — TYPE: USA, California, Shasta Co., Whiskeytown–Shasta–Trinity National Recreation Area, Whiskeytown Unit, ca. 0.8 mi W of Tower House, N side of Willow Creek at junction of Cal. Hwy. 299 with Crystal Creek Road, elev. ca. 500 m, 26 Jul 1988, *Davis* 526 (holotype, BH: isotypes, CAS, NY, US).

Herba perennis, caespitosa, non stolonifera. Caules floriferi 7–40 cm alti. Ligula membranacea, 1.5–2.7 mm longa; lamina involuta, 1.4–2.2 mm lata ubi complanata. Paniculae 2–13 cm longae; rami infimi erecti vel expansi vel horizontales tempore florendi, vel reflexi tempore fructificandi; pedicelli glabri, vel subglabri, scabrelli remote. Gluma prima 0.8–1.9 mm longa, gluma secunda 1.7–2.5 mm longa; lemmata (1–)2–5, lemma primum 2.4–3.3 mm longum.

*P. pumilae* (Vasey) A. Hitchc. affinis, imprimis marginibus lemmatum apices versus scaberulo-serrulatis (non integris nec subintegris), et antheris 1.5–2.0 mm longis (non 0.5–1.0 mm) diversa.



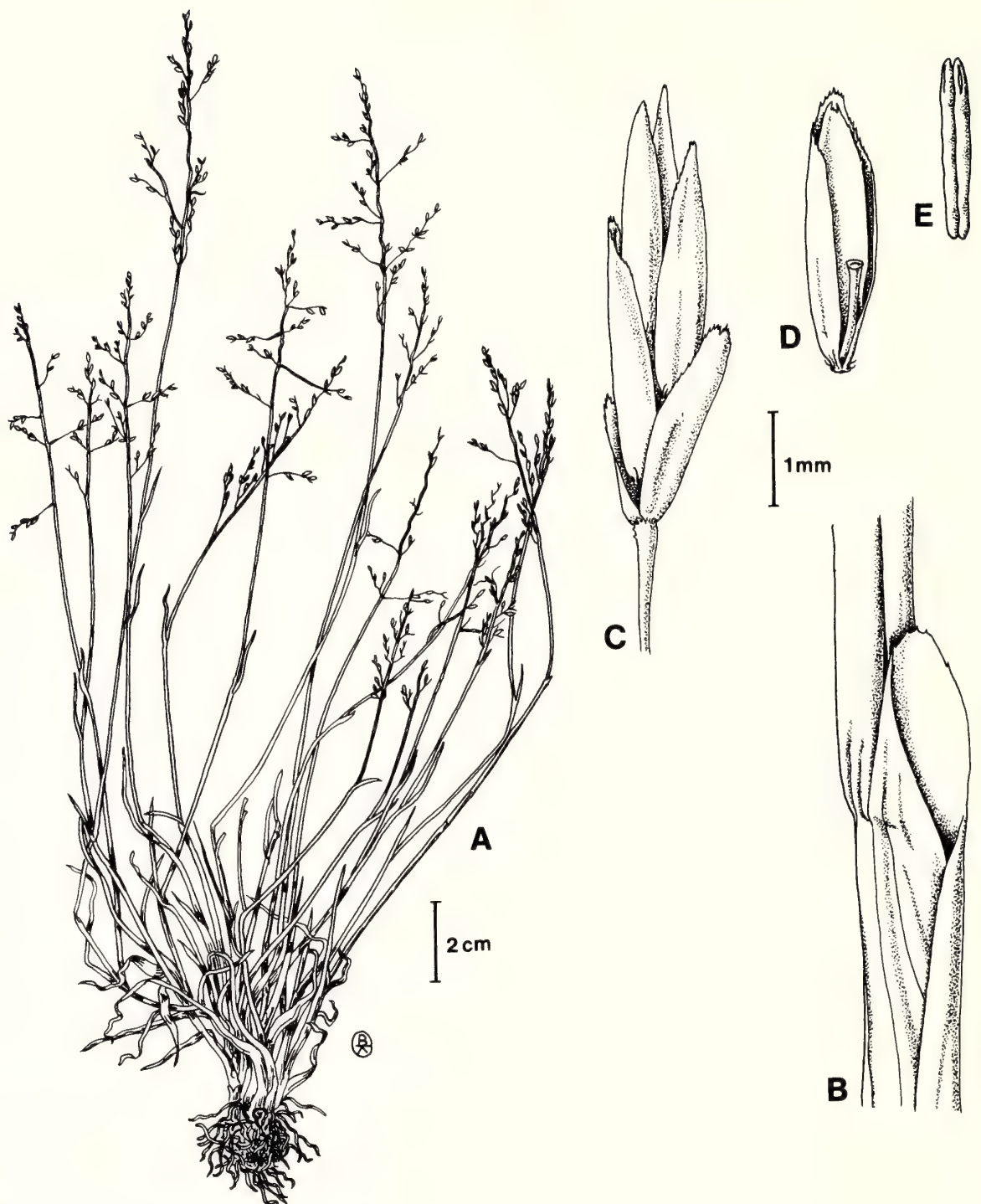


FIG. 1. *Puccinellia howellii* (drawn from Davis 526 [BH]; 2 cm scale applies to A, 1 mm scale to B-E). A. Habit. B. Ligule with associated sections of sheath and blade. C. Spikelet with apex of pedicel. D. Lower floret with rachilla segment. E. Anther of lower floret, partially dehiscent.

Perennial, caespitose, nonstoloniferous herb. Flowering stems ascending to erect, 7–40 cm tall. Leaves basal and cauline; sheath open nearly to base; ligule of cauline leaf membranous, 1.5–2.7 mm long, apex obtuse, margin entire or minutely and irregularly serrate near apex, abaxial surface glabrous to sparsely scabrous near apex, adaxial surface glabrous; blade involute, 1.4–2.2 mm wide when unrolled. Panicles 2–13 cm long, lower branches erect to horizontal at anthesis



and erect to reflexed in fruit, upper branches erect to ascending in flower and in fruit, ultimate branches and pedicels glabrous, or subglabrous with a few scattered scabrules. Spikelets 3.0–7.5 mm long, with (1–)2–5 florets; glumes ovate, usually convex (occasionally keeled), light green to straw brown, often tinged with purple, often banded subapically with yellow near margin, apices acute to obtuse, margins entire below, minutely and uniformly scabrous-serrate near apices, nerves obscure, not converging apically, abaxial surfaces glabrous; first glume 0.8–1.9 mm long, 1-nerved; second glume 1.7–2.5 mm long, (1–)3-nerved; lemmas ovate to elliptic, usually convex (occasionally weakly keeled apically), light green to straw brown, usually tinged with purple, often banded subapically with yellow near margin, apex acute to obtuse, margin entire below, minutely and uniformly scabrous-serrate near apex, nerves 5, obscure, not converging apically, abaxial surface glabrous, or subglabrous with a few hairs near base of lemma, hairs mostly on nerves; lower lemma 2.4–3.3 mm long; palea subequal to lemma, keels 2, glabrous below, glabrous or scabrous near apex. Anthers of lower floret 3, 1.5–2.0 mm long. Caryopses ovoid, tawny to olive green, 1.5–2.0 mm long; embryo 0.4–0.6 mm long.

*Paratypes.* USA, California, Shasta Co. (all from the same locality as the type): 26 Apr 1954, *J. T. Howell* 29177 (CAS [2 sheets], GH, NY, US); 26 Apr 1954, *Rose* 54028 (CAS, DS, GH, NY, RSA, WS, WTU); 14 June 1955, *Howell* 30423 (CAS); 24 Jun 1987, *Martz s.n.* (CAS); 14 Jun 1988, *Martz* 274 (AHUC, BH, CAS, DAV, HSC, RSA, UC).

*Puccinellia howellii* has been collected in flower during April and June, and in fruit during June and July. The holotype bears both mature fruits and dehiscent anthers.

Among described species of *Puccinellia*, *P. howellii* resembles *P. pumila* most closely. The latter species was not mentioned by Munz (1959), and specimens of *P. howellii* and *P. pumila* key in Munz's flora to *P. airoides* (Nutt.) S. Watson & J. Coulter (= *P. nuttalliana* (Schultes) A. Hitchc.), *P. grandis* Swallen (= *P. nutkaensis* (J. S. Presl) Fern. & Weath.), or *P. lemmonii* (Vasey) Scribner. *Puccinellia howellii* and *P. pumila* differ from other species of *Puccinellia* occurring in California in their combination of the following three characters: 1) perennial habit; 2) pedicels glabrous, or subglabrous with a few scattered scabrules (vs. uniformly scabrous, as in *P. distans* (Jacq.) Parl., *P. lemmonii*, *P. nutkaensis*, and *P. nuttalliana*); and 3) keels of the palea glabrous along the lower half (vs. scabrous to scabrous-hispid along the lower half, as in *P. maritima* (Hudson) Parl.). *Puccinellia howellii* differs from *P. pumila* in 1) margin of the lemma near the apex (minutely and uniformly scabrous-serrate in *P. howellii*, entire, or subentire with a few scattered scabrules in *P. pumila*);



and 2) anther length (1.5–2.0 mm in *P. howellii*, 0.5–1.0 mm in *P. pumila*).

*Puccinellia howellii* is known only from the type locality, where it is a dominant element of the vegetation in a series of mineralized seeps, the water from which ranges in conductivity up to 28,000  $\mu\text{mho}/\text{cm}^2$ , and in  $\text{Cl}^-$  concentration up to 10.8 g/liter, the cation content principally  $\text{Na}^+$  (C. Martz, California Dept. of Transportation, pers. comm.). At this site, *P. howellii* occurs in association with other species characteristic of saline and otherwise mineralized soils, including *Juncus bufonius* L., *Spergularia marina* (L.) Griseb., and *Triglochin maritima* L. Most species of *Puccinellia* are endemic to such soils, and most occur either in coastal or in inland sites of this nature (cf. Fernald and Weatherby 1916; Hughes and Halliday 1980; Sørensen 1968; Swallen 1944; Tsvelev 1983). Thus, the habitat of *P. howellii* is not unusual. Notably, the closely related *P. pumila* occurs only in coastal habitats. In California it has been collected in Humboldt Co. (mouth of Eel River, Tracy 16073 [RM, UC, WTU], Rogers 220 [WTU]; Humboldt Bay, Rogers 219 [WTU]), ca. 80 mi from the known population of *P. howellii*.

#### ACKNOWLEDGMENTS

I thank the curators of BH, CAS, DS, GH, NY, RM, RSA, UC, US, WS, and WTU for loans of specimens and for other herbarium services; J. T. Howell for information concerning his collection of *Puccinellia howellii*; C. Martz for the loan of specimens and for information concerning the type locality of *Puccinellia howellii*; B. King for the illustrations; W. Dress for assistance with the Latin description; and K. Nixon, J. R. Reeder, R. Riggins, J. P. Smith, and R. Soreng for comments on drafts of this paper. This work was supported in part by NSF grant BSR 8696101.

#### LITERATURE CITED

- FERNALD, M. L. and C. A. WEATHERBY. 1916. The genus *Puccinellia* in eastern North America. *Rhodora* 18:1–23.
- HUGHES, W. E. and G. HALLIDAY. 1980. *Puccinellia*. Pp. 167–169 in T. G. Tutin, V. H. Heywood, N. A. Burges, D. M. Moore, D. H. Valentine, S. M. Walters, and D. A. Webb (eds.), *Flora Europaea*, Vol. 5. Cambridge Univ. Press, Cambridge, England.
- MUNZ, P. A. 1959. *A California flora*. Univ. of California Press, Berkeley.
- SØRENSEN, T. 1968. *Puccinellia*. Pp. 154–165 in E. Hultén, *Flora of Alaska and neighboring territories*. Stanford Univ. Press, Stanford, CA.
- SWALLEN, J. R. 1944. The Alaskan species of *Puccinellia*. *J. Wash. Acad. Sci.* 34: 16–23.
- TSVELEV, N. N. 1983. *Grasses of the Soviet Union* [Engl. transl. by B. R. Sharma of 1976 Russian ed.]. Amerind Publ. Co., New Delhi.

(Received 4 May 1989; revision accepted 6 Nov 1989.)



## NOTES

**CHROMOSOME COUNTS IN *ASTRAGALUS* (FABACEAE).**—Chromosome counts are reported below for 15 taxa of *Astragalus*. Eleven of these are believed to be previously undocumented. Counts for three of the four previously reported taxa are in agreement with earlier studies (James, L. E., Observations on the taxonomy of *Astragalus*, subgenus *Hesperastragalus*, Contr. Dudley Herb. 4:57–72, 1951; Spellenberg, R., Chromosome numbers and their cytotaxonomic significance for North American *Astragalus* (Fabaceae), Taxon 25:463–476, 1976). A count of “ca.  $n=12$ ” has been reported for *A. breweri* (Raven, P. H., D. W. Khyos, and A. J. Hill, Chromosome numbers of spermatophytes, mostly Californian, Aliso 6:105–113, 1965). This gametic number is in conflict with the gametic and somatic numbers of  $n=11$  and  $2n=22$  obtained in the present study for four populations of this species, including one (*Liston 669-1*) from the same location.

The chromosome numbers reported below support the general homogeneity of section *Inflati*, where most species have  $n=11$  (Spellenberg, loc. cit.). Likewise, the chromosomal heterogeneity of section *Leptocarpi* is further documented, and the first count of  $n=13$  in this section is reported for *A. nyensis*.

The methodology of Soltis (Karyotypic relationships among species of *Boykinia*, *Huechera*, *Mitella*, *Sullivantia*, *Tiarella* and *Tolmiea* [Saxifragaceae], Syst. Bot. 5:17–29, 1980) was used for obtaining mitotic counts from root tips with a cold water (2–4°C) pretreatment of 8–24 hours substituted for 8-hydroxyquinoline. Buds were fixed in 3:1 ethanol:acetic acid (v:v) and meiotic counts were made using standard acetocarmine squash techniques. All counts were documented with drawings made with the aid of a camera lucida and/or photomicrographs. Voucher specimens and documenting drawings are at RSA. Collection numbers are mine unless noted otherwise. Nomenclature and sectional placement follow Barneby (Atlas of North American *Astragalus*, Mem. New York Bot. Gard., 1964). An asterisk denotes a taxon for which the count is believed to be the first reported.

### Sect. *Inflati*

\**Astragalus gruinus* Barneby,  $2n=22$ , Mexico, Baja California, Sierra San Pedro Mártir, Upper Vallecitos, 711-1.

\**A. prorifer* M. E. Jones,  $2n=22$ , Mexico, Baja California, Sierra San Pedro Mártir, 1.6 km E of entrance to Parque Nacional, 772-3.

### Sect. *Leptocarpi*

\**A. acutirostris* S. Watson,  $2n=24$ , CA, Kern Co., 9.6 km N of Hwy 58 on California City Rd, 718-1; San Bernardino Co., Granite Mts., Cottonwood Basin, *Thorne 51550*.

*A. breweri* A. Gray,  $n=11$ , CA, Lake Co., 4.5 km NE of Middletown, 708-1;  $2n=22$ , 5 km NE of Lakeport, 669-1; 13 km S of Hwy 29 on Butts Canyon Rd, 707-1;  $n=11$ , Marin Co., Mt. Tamalpais State Park, Rock Springs, 693-1.

\**A. clarianus* Jepson,  $2n=22$ , CA, Napa Co., Bothe-Napa Valley State Park, 660-1; NE side of Lake Hennessey, Conn Valley Rd, 706-1.

\**A. mohavensis* S. Watson,  $2n=24$ , NV, Clark Co., Spring Mts., mouth of Lee Canyon, *Morefield 4475*.

*A. nothoxys* A. Gray,  $2n=28$ , AZ, Graham Co., Pinaleno Mts., Hwy 366, 7.3 km SW of Hwy 666, 737-1;  $n=14$ , Santa Cruz Co., 8 km SSE of Elgin, 739-1.

*A. nuttallianus* A. DC. var. *imperfectus* (Rydb.) Barneby,  $2n=22$ , NV, Clark Co., N side of Virgin River, 0.5 km SW of Riverside bridge, 729-2.



- \**A. nyensis* Barneby,  $2n=26$ , NV, Clark Co., N side of Virgin River, 0.5 km SW of Riverside bridge, 729-1.
- \**A. pauperculus* E. Greene,  $2n=24$ , CA, Butte Co., 15 km SE of Chico, 694-1; Tehama Co., 5 km SW of Dales, 698-1.
- \**A. rattani* A. Gray var. *rattani*,  $2n=22$ , CA, Mendocino Co., Middle Fork Eel River, 1.4 km SE of Dos Rios, 703-1.
- \**A. rattani* var. *jepsonianus* Barneby,  $2n=22$ , CA, Colusa Co., 10.6 km S of Bartlett Springs Jct. on Bear Valley–Lodoga Rd., 667-3;  $n=11$ , Glenn Co., 5.3 km N of Stonyford on Elk Creek Rd, 699-1;  $2n=22$ , Lake Co., 0.7 km N of Hwy 20 on Walker Ridge Rd, 707-1.
- \**A. tener* A. Gray var. *tener*,  $n=11$ , CA, Merced Co., San Luis Island, 22.4 km N of Los Banos on Hwy 165, 690-1;  $2n=22$ , Solano Co., “Jepson’s Prairie”, S of Lake Olcutt, 691-1.
- A. tener* var. *titi* (Eastw.) Barneby,  $2n=22$ , CA, Monterey Co., Monterey Peninsula, 17 Mile Drive, Bird Rock, *Yadon s.n.*

#### Sect. *Microlobium*

- A. gambelianus* E. Sheldon,  $2n=22$ , CA, Lake Co., 4.5 km NE of Middletown, 708-2.

This research was partially funded by the G. Ledyard Stebbins Award for Research in Evolutionary Botany of the California Native Plant Society and a Dissertation Improvement Grant BSR-8801015 from the National Science Foundation. I thank Lawrence Kelly, Malcolm McLeod, Richard Spellenberg, and Scott Zona for their careful criticism of the manuscript and Mark Blumler, Bill Grummer, Sara Meury, Jim Morefield, and Vern Yadon for their assistance in the field.—AARON LISTON, Rancho Santa Ana Botanic Garden, Claremont, CA 91711. (Received 15 Mar 1989; revision accepted 7 Sep 1989.) Present address: Department of Genetics, University of California, Davis, CA 95616.

---

## NOTEWORTHY COLLECTIONS

### ARIZONA

*ASCLEPIAS CUTLERI* Woodson (ASCLEPIADACEAE).—Apache Co., Nokaito Bench 14.5 km E of Mexican Water Chapter House along S side of old road to Teec Nos Pos and 9.8 km E of US 191,  $36^{\circ}59'30''\text{N}$ ,  $109^{\circ}30'30''\text{W}$ , 1580 m, 15 Jun 1982, *A. M. Phillips, III* (AMP) 82-152 and *N. J. Brian* (MNA); 6.0 km by dirt road SW of Rock Point bridge, dune area E of road, behind small outcrop, locally common,  $36^{\circ}41'\text{N}$ ,  $109^{\circ}40'\text{W}$ , 1670 m, 15 Jun 1982, AMP 82-163 and *Brian* (MNA); 1.6 km W of Rock Point bridge, in sand dunes crossing road,  $36^{\circ}43'\text{N}$ ,  $109^{\circ}39'\text{W}$ , ca. 1600 m, 15 Jun 1982, AMP 82-164B and *Brian* (MNA).

*Previous knowledge.* Originally discovered in 1937 at Nokaito Bench (*Peebles 13581 and Smith*, ARIZ). The Rock Point population, approximately 50 km to the SW, was found in 1938 (*Cutler 2177*; MO, Type). Also known from 3 collections from Grand and San Juan cos., UT (BRY).

*Significance.* Our 1982 collections are apparently the first records of the species in AZ since the original and only known collections were made in 1937–1938. The Rock Point sites were searched in 1981 without finding plants; apparently they remained dormant after the dry winter of 1980–1981, whereas the moist winter of 1981–1982



was sufficient for growth. Listed as a Category 2 Candidate species in U.S. Fish & Wildlife Service Notice of Review (Federal Register, 27 Sep 1985; 50 FR 39526).

*DUDLEYA PULVERULENTA* (Nutt.) Britton & Rose subsp. *ARIZONICA* (Rose) Moran (CRASSULACEAE).—Mohave Co., Lower Granite Gorge of the Grand Canyon, in crevices in schist canyon walls across Colorado River from Separation Canyon, Grand Canyon River Mile 239.5 Left (distance downstream from Lees Ferry), 35°49'N, 113°34'W, about 20 plants, flowering, 300 m, 8 May 1979, *AMP* and *B. G. Phillips* (*BGP*) 79-376 (MNA).

*Previous knowledge.* Nearest previously recorded localities were Yucca, Mohave Co. (type locality of *D. arizonica* Rose) and Newberry Mts., Clark Co., NV.

*Significance.* First record for the Grand Canyon and an eastward range extension of approximately 120 km. Sparsely distributed on canyon walls for about 5 km downstream from Separation Canyon. Locality discovered by S. W. Carothers in 1979.

*ERIOGONUM ZIONIS* J. Howell var. *ZIONIS* (Polygonaceae).—Coconino Co., locally abundant in open woodland in deep, sandy soil on the Paris Plateau with pinyon and juniper, T39N, R4E, sect. 21, 2135 m, 3 Oct 1979, *R. K. Gierisch* 4690 (ASC, ASU); Paria Plateau at top of Vermilion Cliffs, 7.3 km SW of Jarvis Ranch, T39N, R4E, SW¼ sect. 22, 2135 m, 21 Sep 1983, *AMP* and *BGP* 83-352 (MNA).

*Previous knowledge.* Known only from Kane and Washington cos., UT. *Eriogonum zionis* var. *coccineum* J. T. Howell, with red flowers, is locally common at isolated sites along the rims of Kanab Canyon and the Grand Canyon.

*Significance.* First records for AZ.

*EUPHORBIA ERIANTHA* Benth. (EUPHORBIACEAE).—Mohave Co., Peach Springs Wash, 1 km S of junction with Diamond Creek, 520 m, 24 Sep 1972, *T. R. Van Devender* s.n. (ARIZ); along rocky floor of small, steep, dry drainage about 400 m from the Colorado River at Grand Canyon River Mile 215.5 Right, across river from Three Springs Canyon and about 10 River Miles upstream from Diamond Creek, 35°53'N, 113°19'W, in fruit, 490 m, 9 May 1987, *AMP* 87-18 (MNA).

*Previous knowledge.* Distributed in desert areas of Trans-Pecos TX, S, AZ, SE CA, and Mexico (B.C., Son., and Coah.).

*Significance.* First records for the Grand Canyon and Mohave County; northward range extension of about 300 km from nearest known localities in La Paz Co., AZ.

*EUPHORBIA ESULA* L. (EUPHORBIACEAE).—Coconino Co., Kaibab Plateau, in fenced meadow 0.4 km south of Big Springs field station, Kaibab National Forest, along FS route 422, T37N, R1W, SE¼ sect. 13, 2135 m, 18 Jun 1970, *AMP* and *BGP* 53 (ARIZ, ASC, ASU, UNLV), and 29 Sep 1980, *AMP* and *BGP* 80-140 (MNA).

*Significance.* First AZ record for this widely established Eurasian species.

*FLAVERIA MCDUGALLII* Theroux, Pinkava & Keil (COMPOSITAE).—Coconino Co., seep above Colorado River at Grand Canyon Mile 175 Left, 36°14'N, 113°02'W, in open steep drainage, 550 m, 13 Oct 1978, *AMP* 78-778 (MNA); Mohave County, alkaline seeps in 2 levels above Colorado River at Grand Canyon Mile 152 Right, Ledges Camp, about 4 River Miles upstream from mouth of Havasu Creek, 36°21'N, 112°44'W, abundant, 610 m, 10 Apr 1982, *AMP* 82-52 (MNA).

*Previous knowledge.* Species discovered in 1975 by M. E. Theroux at the type locality in Cove Canyon (Mile 174.2 Right). Also known from Matkatamiba Canyon (Mile 148 Left).

*Significance.* Both sites reported here are in moist open situations on slopes and benches above the Colorado River, different habitats from the shaded side canyons where the original collections were made. The Ledges Camp site is a much larger and more extensive population than any of the others; in 1982 it included an area of some 4000 m<sup>2</sup>. Listed as a Category 1 Candidate species in U.S. Fish & Wildlife Service Notice of Review (Federal Register, 27 Sep 1985; 50 FR 39526).



*LEUCOCRINUM MONTANUM* Nutt. (LILIACEAE).—Mohave Co., locally common in open meadow 0.8 km N of Mt. Dellenbaugh fire camp, Shivwits Plateau, 1890 m, 7 Jun 1975, *W. E. Niles and J. S. Holland 592* (UNLV); same locality, T32N, R12W, NW¼ of SE¼ sect. 25, 25 May 1980, *AMP 80-98* (MNA).

*Previous knowledge.* Occurs from OR to MT and S to CA, NV, UT, and NM.

*Significance.* First records for AZ.

*PENSTEMON LAEVIS* Pennell (SCROPHULARIACEAE).—Mohave Co., 8 km by road E of Mt. Trumbull village at junction with Stockade Reservoir Road, roadside and open field, T35N, R9W, SW¼, sect. 21, 1895 m, 5 Jun 1977, *AMP and BGP 77-190* (MNA), det. F. S. Crosswhite, 1977; along Snap Point Road 4.0 km S of junction with Pigeon Canyon Road, T33N, R14W, NW¼ sect. 11, 1370 m, 6 Jun 1977, *AMP and BGP 77-221* (MNA), det. F. S. Crosswhite, 1977; Coconino County, top of Vermilion Cliffs at S edge of Paria Plateau, 7.2 km by road SW of Jarvis Ranch, T39N, R4E, SW¼, sect. 22, 2135 m, 11 Jun 1978, *AMP and BGP 78-586* (MNA), det. N. Holmgren (NY), 1978.

*Previous knowledge.* Kane and Washington cos., UT; in AZ, reported from the Kaibab Plateau, Coconino Co. (Cronquist et al., Intermountain flora, Vol. 4, 1984) at V. T. Park and near Ryan.

*Significance.* Extends the range 110 km W of the Kaibab Plateau to the Arizona Strip and 40 km E to the Paria Plateau.

#### UTAH

*CAMISSONIA EXILIS* (Raven) Raven (ONAGRACEAE).—Kane Co., Coyote Valley, Chinle clay hills on E side of road, 0.2 km N of AZ–UT border, T44S, R2W, NW¼ of SW¼ of NW¼, sect. 9, 1525 m, 28 May 1982, *AMP and BGP 82-103* (MNA).

*Previous knowledge.* Known from Jacobs Ranch, E base of Virgin Mts., Mohave Co., AZ (Munz in 1941, type loc.), and Coyote Valley, Coconino Co., AZ, 0.6 km S of AZ–UT border.

*Significance.* First record for UT. Listed as a Category 2 Candidate species in U.S. Fish & Wildlife Service Notice of Review (Federal Register, 27 Sep 1985; 50 FR 39526).—ARTHUR M. PHILLIPS, III, Museum of Northern Arizona, Route 4, Box 720, Flagstaff, AZ 86001.

#### CALIFORNIA

*ARABIS DISPAR* M. E. Jones (BRASSICACEAE).—Tulare Co., on basalts in an open Jeffrey pine forest with western juniper and *Opuntia basilaris*, Black Mt., Dome Land Wilderness, Sequoia National Forest, T24S, R35E, sect. 7, 7840 ft, 23 May 1981, *Shevock 8589* (CAS, GH) and on granitics in an open Jeffrey pine forest, Rockhouse Basin, Dome Land Wilderness, Sequoia National Forest, T23S, R35E, sect. 25, 6000 ft, 6 Jun 1983, *Shevock 10471* (CAS, GH). Determined by Reed Rollins.

*Significance.* First records for Tulare Co. and the Sierra Nevada. Extends range westward from the Panamint and Argus mts. of Inyo Co. First report for species occurring in a Jeffrey pine forest.

*BRICKELLIA OBLONGIFOLIA* Nutt. var. *LINIFOLIA* (D. Eaton) Robinson (Asteraceae).—Tulare Co., along the Sherman Pass–Blackrock rd in metamorphic rocky soils on the divide between Woodpecker and Rattlesnake Creek drainages, ca. 1 mi S of Bald Mt. Lookout rd jct, Kern Plateau, Sequoia National Forest, T22S, R34E, sect. 11, 8250 ft, 11 Jul 1981, *Shevock 8803* (CAS, RSA). Verified by J. T. Howell.

*Significance.* First record for the Kern Plateau and Tulare Co. Extends range southwestward from east base of Mt. Whitney and eastward from Panamint Mts., Inyo Co.



*HAPLOPAPPUS GILMANII* S. F. Blake (Asteraceae).—Kern Co., base of granitic boulders and gravelly areas in an open mixed conifer forest, east face of Owens Peak along the Sierra Nevada crest, T25S, R35E, sect. 21, 8200 ft, 8 Sep 1987, *Shevock and Jokerst 11809* (CAS, RM, RSA, UC). Verified by Ron Hartman.

*Significance.* First record for the Sierra Nevada and Kern Co. Extends range southwestward ca. 100 km from Telescope Peak, Death Valley, Death Valley National Monument. First report for species on granitics versus limestones.

*HEMITOMES CONGESTUM* A. Gray (Ericaceae).—Kern Co., near the summit of Sunday Peak in a red fir forest, Greenhorn Mts., southern Sierra Nevada, Sequoia National Forest, T25S, R32E, sect. 6, 7840 ft, 2 Sep 1982, *Shevock 10107* (CAS, FSC, MO, RSA).

*Significance.* Southernmost station in CA, and first record for Kern Co. Extends range southward ca. 70 km from Mineral King, Sequoia National Park, Tulare Co.

*LEWISIA DISEPALA* Rydb. (PORTULACEAE).—Kern Co., along sandy-gravelly granitic ridges in an open pinyon pine woodland associated with *Muilla coronata* near Pinyon Peak, Scodie (Kiavah) Mts., Sequoia National Forest, T26S, R36E, sect. 11, 6350 ft, 21 Mar 1984, *Shevock 10799* (CAS).

*Significance.* First record for Kern Co. and first report of species occurring in a pinyon pine woodland. Extends range southward from the disjunct populations on the Sequoia National Forest in Tulare Co. (Lloyd Mdw., Dome Rock, and Church Dome) with the major population center on the domes overlooking Yosemite Valley, Yosemite National Park, Mariposa Co.

*LEWISIA KELLOGGII* M. Brandegee (PORTULACEAE).—Madera Co., along sandy-gravelly ridges of Shuteye Peak, Chiquito Ridge, Sierra National Forest, T7S, R23E, sect. 2, 8250 ft, 2 Jul 1988, *Shevock and Bartel 11840* (CAS).

*Significance.* First record for Madera Co. extending range southward ca. 45 km from the domes overlooking Yosemite Valley, Yosemite National Park, Mariposa Co.

*NOTHOLAENA JONESII* Maxon (ADIANTACEAE).—Fresno Co., occasional on marble-limestone outcrops associated with *Cheilanthes cooperae*, adj. to the Kings River ca. 6 mi E of Mill Flat, Sierra National Forest, T12S, R27E, sect. 26, 1600 ft, *Shevock 11822* (CAS, RSA).

*Significance.* First record for Fresno Co. Extends range northward ca. 44 km from marble outcrops adj. to the Middle Fork Kaweah River, Sequoia National Park, Tulare Co. This calciphile occurs as rare disjunct populations on the Sequoia National Forest from the Piute Mts., Kern Co., northward along the Rincon Fault, Kern River Canyon and in the Tule River Canyon, Tulare Co.

*PHOENICAILIS CHEIRANTHOIDES* Nutt. in Torrey & A. Gray (BRASSICACEAE).—Tulare Co., along the Sherman Pass–Blackrock rd in metamorphic rocky soils on divide between Woodpecker and Rattlesnake Creek drainages, ca. 1 mi S of Bald Mt. lookout rd jct, Kern Plateau, Sequoia National Forest, T22S, R34E, sect. 11, 8250 ft, 27 Jun 1977, *Shevock 5587* (CAS, RSA).

*Significance.* First record for Tulare Co. and Kern Plateau. Extends range southwestward from Big Pine Creek, eastern slope of the Sierra Nevada, Inyo Co.

*TRAUTVETTERIA CAROLINIENSIS* (Walter) Vail var. *OCCIDENTALIS* (A. Gray) C. Hitchc. [*T. grandis* Nutt. ex Torrey & A. Gray in *A California Flora*] (RANUNCULACEAE).—Fresno Co., openings and damp areas in a red fir forest adj. to banks of Rancheria Creek below jct of Little Rancheria Creek, North Fork Kings River drainage, Sierra National Forest, T11S, R28E, sect. 19, 6800 ft, 21 Jul 1989, *Shevock and Clines 11874* (CAS, FSC, NY, RSA, UC, US).



*Significance.* First record for the southern Sierra Nevada. Extends range southward ca. 425 km from Bucks Lake area in Plumas Co. according to herbarium records at CAS, DS, JEPS, and UC. Knowledge of this range extension initially came to the author's attention while reviewing a set of unmounted specimens at CAS (obtained primarily from the southern Sierra Nevada) where the collector's name became separated from the specimens. Based on some detective work, it was later determined that the original specimen documenting this noteworthy collection was obtained on 24 Jul 1985 by *Rick Villaseñor s.n.*—James R. Shevock, Dept. of Botany, California Academy of Sciences, San Francisco, CA 94118-4599.

*ARABIS PINZLAE* Rollins (BRASSICACEAE).—Mono Co.: Inyo Natl. For., White Mts., Fishlake Valley drainage, N facing S slope of the canyon of the North Fork of Chiatovitch Cr., above upper spring, 1.8 mi [2.9 km] N 55° E of Mt. Dubois summit, T2S R33E, SW ¼ of sect. 3, 10,600 ft [3230 m], 8 Jul 1987, *Morefield 4584 and Elias* (GH, RSA). Verified against type material at NSMC, with thanks to Dr. Ann Pinzl, Curator.

*Previous knowledge.* Known only from the type locality in the White Mts., on the NE slope of Boundary Peak in Esmeralda Co., NV (Rollins, Contrib. Gray Herb. 212:110, 1982).

*Significance.* First collection in CA, an extension 7 km SSE from the type locality. This plant should be considered rare in CA, but not particularly threatened since it occurs only on, and appears adapted to, steep unstable scree and sand above 3000 m. A second NV population also has been discovered: ca. 1.6 km ENE of the type locality, *Morefield 4656* (BRY, GH, K, MICH, MO, NSMC, NY, RSA, UC). *Arabis pinzlae* is closely related to, and generally grows with, *A. platysperma* A. Gray var. *platysperma*. Some plants from the new NV population appear intermediate in being more sparsely pubescent at maturity, and somewhat more robust, than "typical" *A. pinzlae*. The two taxa may not be as distinct as first suggested.

*CAREX INCURVIFORMIS* Mackenzie (CYPERACEAE).—Mono Co.: Inyo Natl. For., White Mts., S rim of Pellisier Flats, drying frost-heaved sod hummocks in meadow on NE shoulder of Mt. Hogue, 3.7 mi [6.0 km] S 47° E of Mt. Dubois summit, T2S R33E sect. 26 NE ¼, 12,390 ft [3775 m], 28 Jul 1988, *Morefield 4831 and Perala* (BRY, MICH, MO, NY, RSA, UC).

*Previous knowledge.* *Carex incurviformis* var. *incurviformis* is an uncommon alpine sedge of the Canadian Rockies in SE British Columbia and SW Alberta. The var. *danaensis* (Stacey) F. J. Hermann is a rare plant from the Sierra Nevada of Inyo, Tulare, and Tuolumne cos., CA, with one disjunct station in Park Co., CO, at 12,000–13,000 ft. Both taxa are very close to *C. maritima* Gunnerus. (Leaf. W. Bot. 2(9): 166–167, 1939; Leaf. W. Bot. 7(12):287–289, 1955).

*Significance.* In stature, inflorescence density, and scale shape, the new records appear intermediate between vars. *danaensis* and *incurviformis*, though somewhat closer to the former. As the latter, the new plants would be the first report for CA and the U.S.A.; as the former, they would represent the first report for Mono Co. and the Great Basin, helping to fill a large geographic gap in a rare taxon nearly endemic to the Sierra Nevada.

*CAREX NORVEGICA* A. J. Retzius [including *C. media* R. Brown] (CYPERACEAE).—Mono Co.: Inyo Natl. For., White Mts., wet protected places along stream in side canyon on S side of cirque at head of Indian Cr., 2.6 mi [4.2 km] N 76° E of Mt. Hogue summit, T2S R34E sect. 30 E ½, 9350 ft [2850 m], 1 Aug 1988, *Morefield 4850* (BRY, LE, MEXU, MICH, MO, NSW, NY, PE, RSA, UC); head of E branch of S fork of upper Middle Cr., Fishlake Valley drainage, T2S R33E sect. 4, 11,100 ft [3380 m], 23 Aug 1986, *Taylor 8851* (RSA).

*Significance.* First CA reports for this circumboreal species, a disjunct extension ca. 600 km W from the nearest known site in Garfield Co., UT, and ca. 800 km SW



from ID. The species still is not known from intervening NV, but the new reports are within 2 miles of the state line.

*DRABA MONOENSIS* Rollins and Price (BRASSICACEAE).—Mono Co.: Inyo Natl. For., White Mts., in moist dense sod of small E sloping spring meadow on E rim of Pellisier Flats at head of S Fork of Chiatovitch Cr., 1.2 mi [1.9 km] S 41° E of Mt. Dubois summit, T2S R33E sect. 16 SE ¼, 13,080 ft [3990 m], 28 Jul 1988, *Morefield 4834 and Perala* (BRY, GH, MICH, MO, NY, RSA, UC).

*Previous knowledge.* Recently described (Aliso 12(1):22–24, 1988) as narrowly endemic to the White Mts. of Mono Co., all cited populations occurring along a 5 km section of the main divide between Mt. Barcroft and White Mountain Pk.

*Significance.* The new disjunct population appears to be the largest known for the species, and extends its range 18 km NNW. Plants in the new population were growing abundantly and luxuriantly in a moist isolated ca. 50 m<sup>2</sup> meadow otherwise dominated by *Carex* spp. Average density was estimated visually at 100–200/m<sup>2</sup>; no plants were seen adjacent to the meadow. All other populations seen have consisted of a very few widely scattered individuals. As noted in the original description, *Draba monoensis* is dimorphic for density of stem pubescence, with about 40% of the plants glabrous or sparsely pubescent, and 60% densely pubescent. A similar ratio was observed in the new population. The new population notwithstanding, *Draba monoensis* should be considered rare and at least threatened throughout its small range. Rollins and Price (1988) noted three *Draba* largely endemic to the White Mts., but *Draba monoensis* is by far the rarest. All known populations occur in moist soil subject to disturbance, either along White Mountain Road or in places attractive to grazing animals. Cattle are capable of reaching most of the known populations, and feral horses were observed near the new population.

This note is second in a series based on collections from the White Mts. In the first (Madroño 35(2):164–166, 1988), *Taylor 8851* was cited in error under *Carex parryana* var. *hallii* (see *C. norvegica* above). The other report for that taxon remains valid.—JAMES D. MOREFIELD, Rancho Santa Ana Botanic Garden, 1500 N. College Ave., Claremont, CA 91711-3101; and DEAN WM. TAYLOR, Biosystems Analysis Inc., 303 Potrero St. Suite 29-203, Santa Cruz, CA 95060.

## ANNOUNCEMENT

### NEW PUBLICATIONS

LEVIN, G. A. and R. MORAN. 1989. *The vascular flora of Isla Socorro, Mexico*. 71 pp. San Diego Natural History Museum Memoir 16. \$11.00 + postage and handling (\$1.50 in USA, \$2.50 foreign) + \$0.66 (sales tax for California residents). Send orders to Library, San Diego Natural History Museum, P.O. Box 1390, San Diego, CA 92112. [The Revillagigedos Islands, located south of the Baja California Peninsula, are sometimes considered the Galapagos of the north. The islands are of much interest to biogeographers and conservationists because of their isolated position, endemism, and the threats to their biota. The systematic portion of the *Flora* includes keys, descriptions, and distributions for the plants of Isla Socorro, the largest island of the archipelago. Several new taxa are described and illustrated. The book also contains discussions of vegetation, biogeography, and of the impacts of human settlement and introduced species. Appendices list the floras of other islands of the archipelago.]



## ANNOUNCEMENT

## NEW PUBLICATIONS

AIKEN, S. G., P. F. LEE, D. PUNTER, and J. M. STEWART. Wild rice in Canada. *Research Branch, Agriculture Canada* 1830:1–130 (incl. 4 color pls.), 1988, ISBN 1-55021-027-0, Can\$18.95 Canada, US\$22.75 foreign (from Canadian Govt. Publishing Centre, Supply and Services Canada, Ottawa K1A 0S9). [Contents: intro.; morphology of *Zizania*; taxonomy of idem (4 spp., 6 var., with keys); habitat; management of natural stands; diseases and pests; harvesting and processing the grain; the wild rice industry; biblio.; glossary; index. Based on William G. Dore's "Wild rice," Ibid. publ. 1371:1–84 (1969).]

BOCK, JANE H. and YAN B. LINHART (eds.). *The evolutionary ecology of plants*. Westview Press, 5500 Central Ave., Boulder, CO 80301, Aug. 1989, xiii, 600 pp., ISBN 0-8133-7464-2 (hardbound), price unknown, same ISBN (paperbound), \$44.00. [Mostly the proceedings of a symposium held Aug. 1987 in Columbus, OH, with 28 articles (many deal with western North American plants) in 7 topic areas, this is a splendid testimonial to Herbert G. Baker, the dean of evolutionary biology, by his associates and especially students.]

CODY, WILLIAM J. Plants of Riding Mountain National Park, Manitoba. *Research Branch, Agriculture Canada* 1818/E:[i–vii], 1–319[320], 1988, ISBN 0-660-12879-9, Can\$24.75 Canada, US\$55.80 foreign (for address see entry for Aiken et al.). [Contents: familial key; flora (88 fam., 300 gen., 669 spp., 2 hybrids vascular plants); excluded spp.; biblio.; checklist of species; glossary; index. Also in French as "Flore du Parc national du mont Riding, Manitoba," Ibid. publ. 1818/F.]

DUKE, JAMES A. *CRC handbook of nuts*. CRC Press, 2000 Corporate Blvd. NW, Boca Raton, FL 33431, 1989, [xviii], 343 pp., illus., ISBN 0-8493-3636-8 (hardbound), \$175.00 U.S., \$205.00 foreign, post-paid. [On 109 species, incl. such as *Simmondsia chinensis* and *Pinus edulis*.]

EBELING, WALTER. *Handbook of Indian foods and fibers of arid America*. University of California Press, 2120 Berkeley Way, Berkeley, CA 94720, 1986, xxviii, 971 pp., illus., ISBN 0-520-05436-9 (hardbound), \$79.95. [Contents: the first Americans; the Great Basin; Owens Valley (California, Nevada); California; lower Colorado River Basin; sw U.S.; Mexico; historical perspective; 59-p. appendix (plant species used by Indians, arranged by families); glossary; 48-p. biblio.; index. Most of book deals with plant materials (usually arranged by family in the aforementioned regions), with brief descriptions of species and then ethnobotanical details. Extended sections also treat crop techniques, water use, various Indian cultures, and faunal/fish aspects. This monumental synthesis of ethnobotany of prehistoric and historic Indians of the U.S. and Mexico should quickly become a classic.]



HALL, CLARENCE A., JR. and VICTORIA DOYLE-JONES (eds.). *Plant biology of eastern California: The Mary DeDecker Symposium*. White Mountain Research Station, 6713 Geology Bldg., Los Angeles, CA 90024-1567, Sep. 1988, [i], iii, 364 pp., illus., no ISSN/ISBN, paperbound, \$15.00 postpaid. [= *Natural History of the White-Inyo Range, Symposium Volume 2*. Proceedings of a symposium held 1987 to honor Mary DeDecker (b. 1909), with 28 articles, e.g.: J. D. Morefield on floristic habitats of the White Mts. (WM); R. A. Price and R. C. Rollins on *Draba* (Cruc.) in WM, etc.; A. M. Peterson and D. L. Elliott-Fisk on phytogeography of deciduous trees in WM; D. K. Bailey: single-needle pinyon pines—three taxa, not one; T. P. Spira and L. K. Wagner on weedy annuals in the alpine zone of WM; H. C. Forbes et al. on vegetation (V) and flora of Fish Slough area; S. Jennings on late Quaternary V changes in WM; R. M. Norris on Eureka Valley sand dunes; Elliott-Fisk and A. D. Ryerson on dendrochronological potential of E-central California; B. Ertter on C. A. Purpus's 1895–1898 collecting trips; Morefield et al. on an updated checklist of the flora of WM (1078 taxa, 317 since 1973); no index. Vol. 1 = Clarence A. Hall, Jr. and Donna J. Young (eds.), *Natural history of the White-Inyo Range, eastern California and western Nevada, and high altitude physiology*, 1986, vii, 240 pp., 1 pl. (color), text illus. (B&W), with 29 articles.]

STEWART, CHARLES. *Wildflowers of the Olympics and Cascades*. Nature Education Enterprises, 5016 Old Mill Rd., Port Angeles, WA 98362, Apr. 1988, [122] pp., illus. (most color), no ISBN, paperbound, \$9.95. [An updating of Stewart's *Wildflowers of the Olympics* (1972); enhanced with 194 largely excellent color photographs (two per page) treating 192 species of angiosperms, most of which occur elsewhere—91 in Alaska, 170 in British Columbia, 180 in Oregon, 150 in California. Several dozen other plants receive incidental mention. This is a fair percentage of the ca. 1450 species and subspecific taxa (in over 100 families) of vascular plants that Nelsa M. Buckingham and Edward L. Tisch cataloged for the area—Vascular plants of the Olympic Peninsula, Washington (a catalog), *University of Washington/Co-operative Park Studies Unit Report B-79-2*:[i], i–ii, 1–74, 1979.]

VANDER KLOET, S. P. The genus *Vaccinium* in North America. *Research Branch, Agriculture Canada* 1828:i–xi, 1–201, 1988, ISBN 0-660-13037-8, Can\$46.50 Canada, US\$55.80 foreign (for address see entry for Aiken et al.). [Contents: general discussion on cultivation, distribution, growth, pollination, dispersal, mycorrhizae, evolution, classification; taxonomic part (10 sect., 26 spp.); appendices (herbaria and collection sites; synonymy for species names); biblio.; species index.]



## ANNOUNCEMENT

### XV INTERNATIONAL BOTANICAL CONGRESS TOKYO

The Organizing Committee of the XVth International Botanical Congress announces that the XV IBC will be held in the Tokyo area during August and September, 1993: nomenclatural session 23–27 August; general session 28 August–3 September. The first circular of the XV IBC will be prepared in 1990 and distributed to those interested in the Congress. Requests for information and other questions and comments may be sent to: The Secretariat, XV International Botanical Congress Tokyo, Department of Botany, Faculty of Science, The University of Tokyo, 7-3-1 Hongo, Bunkyo-ku, Tokyo 113, Japan.



## SUBSCRIPTIONS—MEMBERSHIP

Membership in the California Botanical Society is open to individuals (\$22 per year; students \$12 per year for a maximum of seven years). Members of the Society receive MADROÑO free. Family memberships (\$25) include one five-page publishing allotment and one journal. Emeritus rates are available from the Corresponding Secretary. Institutional subscriptions to MADROÑO are available (\$30). Membership is based on a calendar year only. Applications for membership (including dues), orders for subscriptions, and renewal payments should be sent to the Treasurer. Requests and rates for back issues, changes of address, and undelivered copies of MADROÑO should be sent to the Corresponding Secretary.

## INFORMATION FOR CONTRIBUTORS

Manuscripts submitted for publication in MADROÑO should be sent to the editor. All authors must be members, and membership is prerequisite for review.

Manuscripts may be submitted in English or Spanish. English-language manuscripts dealing with taxa or topics of Latin America and Spanish-language manuscripts must have a Spanish RESUMEN and an English ABSTRACT.

Manuscripts and review copies of illustrations must be submitted in triplicate for all articles and short items (NOTES, NOTEWORTHY COLLECTIONS, POINTS OF VIEW, etc.). Follow the format used in recent issues for the type of item submitted. Allow ample margins all around. Manuscripts **MUST BE DOUBLE SPACED THROUGHOUT**. For articles this includes title (all caps, centered), author names (all caps, centered), addresses (caps and lower case, centered), abstract and resumen, text, acknowledgments, literature cited, tables (caption on same page), and figure captions (grouped as consecutive paragraphs on one page). Order parts in the sequence listed, ending with figures. Each page should have a running header that includes the name(s) of the author(s), a shortened title, and the page number. Do not use a separate cover page or “erasable” paper. Avoid footnotes except to indicate address changes. Table and figure captions should contain all information relevant to information presented. All measurements and elevations should be in metric units. Specimen citations may include English or metric distance measurements.

Line copy illustrations should be clean and legible, proportioned (including captions) to the MADROÑO page, and designed for reduction to  $\frac{2}{3}$  original size. Scales should be included in figures, as should explanation of symbols, including graph coordinates. Symbols smaller than 1 mm after reduction are not acceptable. Maps must include latitude and longitude references. Halftone copy should be designed for reproduction at actual size. In no case should original illustrations be sent prior to the acceptance of a manuscript. When needed they should be mounted on stiff cardboard and sent flat. No illustrations larger than 22 × 28 cm will be accepted.

Presentation of nomenclatural matter (accepted names, synonyms, typification) should follow the format used for members of the *Allium sanbornii* complex in MADROÑO 36:124–128. 1989. Institutional abbreviations in specimen citations should follow Holmgren, Keuken, and Schofield, *Index Herbariorum*, 7th ed. Names of authors of scientific names should be abbreviated according to the *Kew Draft Index of Author Abbreviations* (1980). Abbreviation of serial titles should be those in *Botanico-Periodicum-Huntianum* (Lawrence et al., 1968, Hunt Botanical Library, Pittsburgh). If the correct abbreviation cannot be determined, the full serial title should be used. Titles of books should be given in full, together with the place and date of publication, publisher, and edition, if other than the first.

All members of the California Botanical Society are allotted five free pages per volume in MADROÑO. Joint authors may split the full page number. Beyond that number of pages a required editorial fee of \$65.00 per page will be assessed. The purpose of this fee is not to pay directly for the costs of publishing any particular paper, but rather to allow the Society to continue publishing MADROÑO on a reasonable schedule, with equity among all members for access to its pages. Printer's fees for illustrations and typographically difficult material @ \$35.00 per page (if their sum exceeds 30 percent of the paper) and for author's changes after typesetting @ \$4.50 per line will be charged to authors.

At the time of submission, authors must provide information describing the extent to which data in the manuscript have been used in other papers that are published, in press, submitted, or soon to be submitted elsewhere.





## CALIFORNIA BOTANICAL SOCIETY

### STATEMENT OF OWNERSHIP, MANAGEMENT, AND CIRCULATION

(Required by Title 39, U.S.C. 3685)

MADROÑO, A West American Journal of Botany, is published quarterly at Berkeley, California. Annual subscription price is \$30.00.

The Publisher is the California Botanical Society, Inc., University Herbarium, Life Science Building, University of California, Berkeley, CA 94720.

The editor is David J. Keil, Biological Sciences Department, California Polytechnic State University, San Luis Obispo, CA 93407.

The owner is the California Botanical Society, Inc., University Herbarium, Life Science Building, University of California, Berkeley, CA 94720. There are no bondholders, mortgagees, or other security holders.

The average number of copies distributed of each issue during the preceding 12 months is 1075; the number of copies of the single issue closest to the filing date is 1094. The net press run is 1250 copies.

I certify that the statements made by me above are correct and complete.

3 October 1989

DAVID J. KEIL, *Editor*



QK  
1  
m183  
Bot.

## MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

## Contents

|  |                   |
|--|-------------------|
| FOREST ASSOCIATIONS OF LITTLE LOST MAN CREEK, HUMBOLDT COUNTY, CALIFORNIA:<br>REFERENCE-LEVEL IN THE HIERARCHICAL STRUCTURE OF OLD-GROWTH COASTAL<br>REDWOOD VEGETATION<br><i>James M. Lenihan</i>                     | 69                |
| FOREST HABITAT TYPES OF THE SOUTH WARNER MOUNTAINS, MODOC COUNTY,<br>CALIFORNIA<br><i>Gregg M. Riegel, Dale A. Thornburgh, and John O. Sawyer</i>  | 88                |
| AN INVESTIGATION INTO THE STATUS OF <i>IRIS THOMPSONII</i> (IRIDACEAE)<br><i>Carol A. Wilson, Alfred Levinson, and Richard Petersen</i>  | 113               |
| COMMENTS ON SOUTHWESTERN UNITED STATES <i>EVOLVULUS</i> AND <i>IPOMOEA</i><br>(CONVOLVULACEAE)<br><i>Daniel F. Austin</i>  | 124               |
| PRESENT STATUS OF <i>AMBLYOLEPIS</i> (ASTERACEAE: HELIANTHEAE)<br><i>Mark W. Bierner</i>   | 133               |
| CHROMOSOME COUNTS IN SECTION <i>SIMIOLUS</i> OF THE GENUS <i>MIMULUS</i><br>(SCROPHULARIACEAE). XI. <i>M. GLABRATUS</i> COMPLEX (CONT.)<br><i>Robert K. Vickery, Jr., Fahima Rahman, Steven R. Pack, and Thong Mac</i> | 141               |
| NOTES<br><i>BRAYA GLABELLA</i> VAR. <i>GLABELLA</i> (BRASSICACEAE) IN COLORADO<br><i>Barbara A. Siems and Elizabeth E. Neely</i>   | 146               |
| NOTEWORTHY COLLECTIONS<br>CALIFORNIA<br>WYOMING<br>WASHINGTON  | 112<br>140<br>144 |
| REVIEW   | 147               |
| ANNOUNCEMENTS  | 148               |



MADROÑO (ISSN 0024-9637) is published quarterly by the California Botanical Society, Inc., and is issued from the office of the Society, Herbarium, Life Sciences Building, University of California, Berkeley, CA 94720. Subscription rate: \$30 per calendar year. Subscription information on inside back cover. Established 1916. Second-class postage paid at Berkeley, CA, and additional mailing offices. Return requested. POSTMASTER: Send address changes to James R. Shevock, Botany Dept., California Academy of Sciences, San Francisco, CA 94118.

*Editor*—DAVID J. KEIL

Biological Sciences Department  
California Polytechnic State University  
San Luis Obispo, CA 93407

*Board of Editors*

Class of:

- 1990—STEVEN TIMBROOK, Ganna Walska Lotusland Foundation, Montecito, CA  
THOMAS R. VAN DEVENDER, Arizona-Sonora Desert Museum, Tucson, AZ  
1991—JAMES HENRICKSON, California State University, Los Angeles, CA  
WAYNE R. FERREN, JR., University of California, Santa Barbara, CA  
1992—BRUCE A. STEIN, The Nature Conservancy, Washington, D.C.  
WILLIAM L. HALVORSON, Channel Islands National Park, Ventura, CA  
1993—JON E. KEELEY, Occidental College, Los Angeles, CA  
RHONDA L. RIGGINS, California Polytechnic State University, San Luis Obispo, CA

---

CALIFORNIA BOTANICAL SOCIETY, INC.

OFFICERS FOR 1989-90

- President:* ROBERT W. PATTERSON, Biological Sciences Department, San Francisco State University, San Francisco, CA 94132  
*First Vice President:* NIAL F. MCCARTEN, Department of Integrative Biology, University of California, Berkeley, CA 94720  
*Second Vice President:* MARY L. BOWERMAN, 970 Second Street, Lafayette, CA 94549  
*Recording Secretary:* RODNEY G. MYATT, Department of Biological Sciences, San Jose State University, San Jose, CA 95192  
*Corresponding Secretary:* BARBARA ERTTER, University Herbarium, University of California, Berkeley, CA 94720  
*Treasurer:* MONA BOURELL, Department of Botany, California Academy of Science, San Francisco, CA 94118  
*Financial Officer:* BARRETT ANDERSON, Department of Botany, California Academy of Science, San Francisco, CA 94118

The Council of the California Botanical Society consists of the officers listed above plus the immediate *Past President*, JOHN STROTHER, University Herbarium, University of California, Berkeley, CA 94720; the *Editor* of MADROÑO; three elected *Council Members*: JAMES SHEVOCK, Department of Botany, California Academy of Science, San Francisco, CA 94118; ELIZABETH MCCLINTOCK, University Herbarium, University of California, Berkeley, CA 94720; BRUCE PAVLIK, Department of Biology, Mills College, Oakland, CA 94613; and a *Graduate Student Representative*, JAMES D. MOREFIELD, Rancho Santa Ana Botanic Garden, Claremont, CA 91711.

|   |
|---|
| THIS PUBLICATION IS PRINTED ON ACID-FREE PAPER. |
|---|



# FOREST ASSOCIATIONS OF LITTLE LOST MAN CREEK, HUMBOLDT COUNTY, CALIFORNIA: REFERENCE-LEVEL IN THE HIERARCHICAL STRUCTURE OF OLD-GROWTH COASTAL REDWOOD VEGETATION

JAMES M. LENIHAN

Department of Geosciences, Oregon State University,  
Corvallis, OR 97331

## ABSTRACT

Vegetation structure, floristic composition, and several topographic and edaphic factors were measured in eighty old-growth coastal redwood (*Sequoia sempervirens*) stands in the Little Lost Man Creek Research Natural Area, Redwood National Park, CA. Multivariate classification techniques were used to classify the sample stands and characterize the forest associations in terms of structure and composition. The associations formed a toposequence presumably related to microclimatic, edaphic, and disturbance gradients in the natural area. Three associations were defined: the *Sequoia sempervirens*/*Blechnum spicant* association at lower elevations on concave lower slopes; the *Sequoia sempervirens*/*Arbutus menziesii* association at higher elevations on convex upper slopes and ridgetops; and the *Sequoia sempervirens*/*Mahonia nervosa* association at intermediate positions along the toposequence. Ecological relationships in the study area and throughout the coastal redwood forest are viewed in the context of a gap-association-watershed-region hierarchy. Vegetation pattern and process in the redwood region show a certain symmetry across scale characteristic of scaling fractals.

The Little Lost Man Creek watershed in Redwood National Park was designated a research natural area in 1973 by the National Park Service to represent virgin, upland coastal redwood (*Sequoia sempervirens*) forest in the northern part of its range. This study defines old-growth forest associations in the natural area in terms of structure, composition, and distribution along a topographic gradient. The forest-type classification partitions vegetation into subunits delimiting relatively uniform habitats, and thus provides a framework for future ecological research in the natural area.

The forest associations of Little Lost Man Creek also serve as a reference level from which to view the hierarchical structure of redwood vegetation. From this perspective, each association is a patchwork of different-aged forest gaps, the associations are patches at the scale of the watershed, and watersheds comprise the redwood forest at the regional scale. By viewing the associations in the context of a hierarchical structure, a conceptual framework is available for understanding the development and dynamics of vegetation pattern in the study area. Hierarchical theory (Allen and Starr 1982; Allen et al. 1984; O'Neill et al. 1986; Urban et al. 1987) predicts that



reference-level processes (e.g., ecological processes at the association-level) are constrained by processes at the next higher level in the hierarchy (e.g., the watershed-level) and have their mechanistic explanation in processes at the next lower level (e.g., the forest gap-level).

Coastal redwood vegetation, like all vegetation, is fractal because it exhibits structure at all spatial scales of interest (Palmer 1988). This study and related studies show that pattern and process in redwood vegetation at three different levels of the hierarchy (i.e., regional, watershed, and association-levels) exhibit a symmetry across scale. This suggests redwood vegetation is to some extent self-similar, a property characteristic of a special subset of fractals called "scaling" fractals (Mandelbrot 1983).

### STUDY AREA

The relatively undisturbed, 972 ha study area is located in northern Humboldt County, California (Fig. 1). Little Lost Man Creek is a perennial stream in the greater Redwood Creek drainage basin (California Dept. of Water Resources 1965). The watershed is a mature landform with a deeply-incised ravine, steep lower slopes, more moderate upper slopes, and a well-defined ridgeline. Numerous intermittent streams dissect the slopes of the watershed, and there is one major perennial tributary in the upper southeast corner of the watershed. Elevations range from 30 m at the mouth of the creek to 732 m in the upper southeast corner of the watershed.

The research natural area is located at the northern end of the Coast Range Province in the central belt of the Franciscan Formation (Irwin 1960). The most common rocks in the study area are gray-wacke sandstones, shales, and conglomerates. The majority of soils in the study area are classified as Melbourne clay loams or Hugo loams (DeLapp et al. 1961a, b; DeLapp and Smith 1977). Melbourne clay loams are fine, mixed, mesic ultic haploxeralfs and Hugo loams are fine, loamy, mixed mesic dystric xerochrepts.

The climate is maritime Mediterranean with cool, rainy winters and cool, dry summers. The mean daily maximum temperature in July is 21°C with absolute maxima rarely exceeding 35°C (Elford and McDonough 1974). The mean daily minimum in January is 4°C. Absolute minima rarely go below -8°C. About 90% of the annual precipitation falls between October and May. Average annual rainfall is about 1800 mm. Light snowfall is common in the study area at higher elevations during winter months. Heavy, wet fog produced by onshore movement of moist oceanic air is a common feature of the climate in the summer. Fog often persists for all but a few hours in the afternoon at lower elevations, but a warm inver-



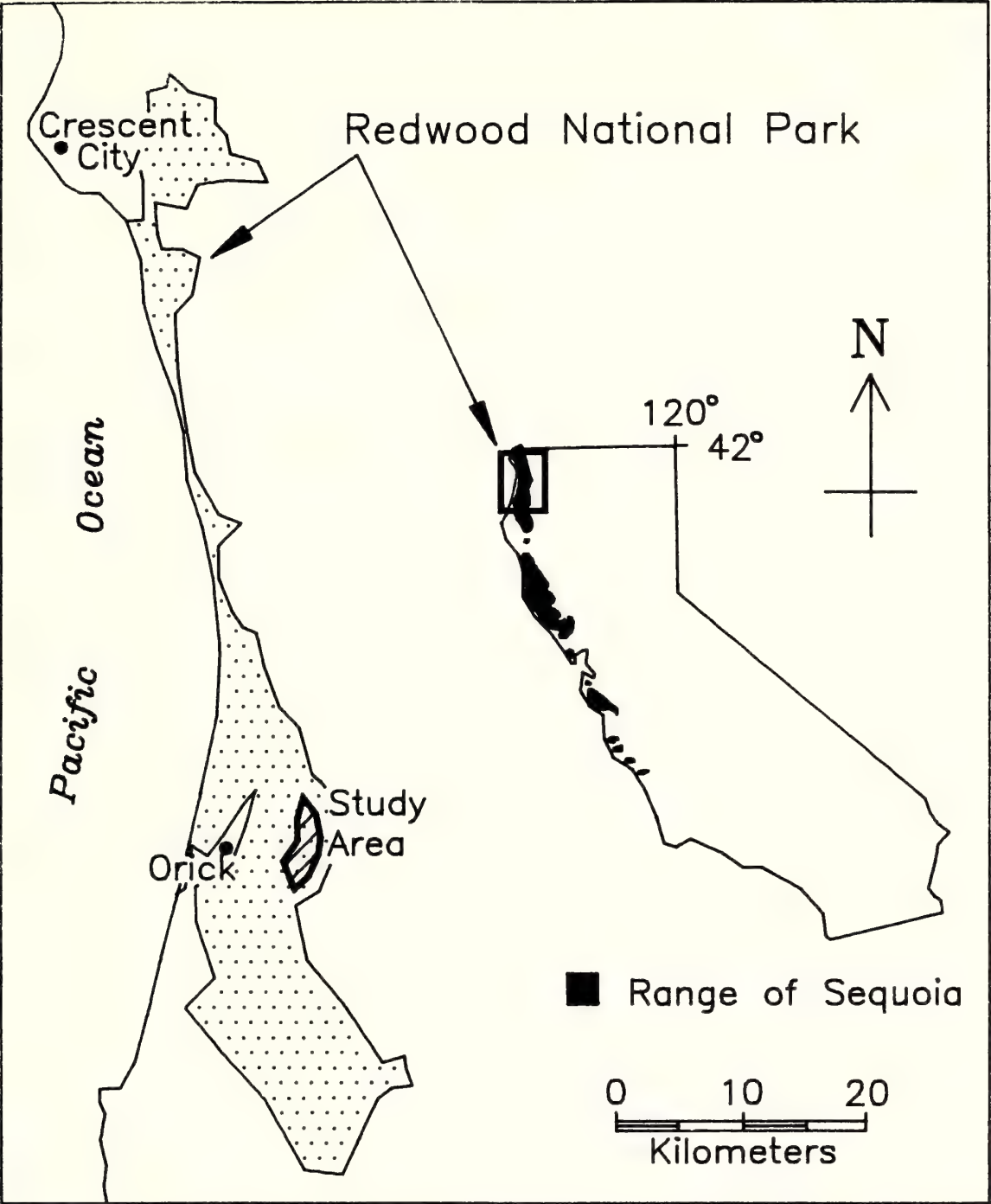


FIG. 1. Location of the study area in Redwood National Park, the location of Redwood National Park in California, and the distribution of coastal redwood (*Sequoia sempervirens*).

sion layer forms during the summer months at about 450 m, so fog is less common above this altitude (Freeman 1971). A water balance diagram (Thornthwaite and Mather 1957; Fig. 2) based on climatic data near the research natural area (Elford and McDonough 1974) shows a climate characterized by a long wet season with a large water surplus and a short dry season with a slight water deficit. These features are typical of the climate throughout the coastal coniferous forest belt of the Pacific Northwest (Walter et al. 1975).



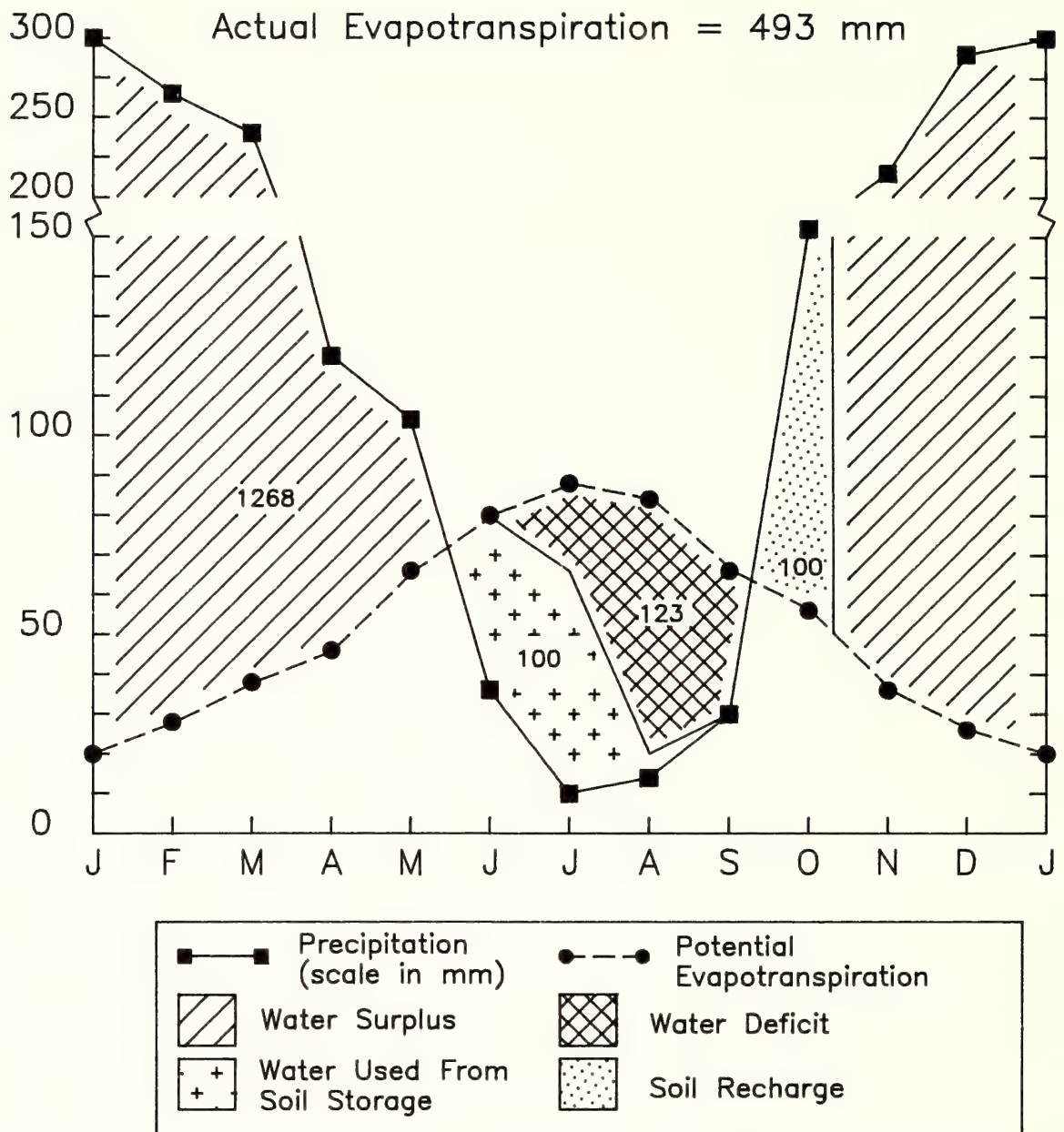


FIG. 2. Water balance diagram for the Orick-Prairie Creek, CA, weather station representing the climate of the study area. All measurements are in mm. Calculations assumed 100 mm of available soil water storage.

## METHODS

One hundred potential sample points were located by overlaying a dot grid on a 7.5 minute topographic map of the watershed. Dots were spaced at intervals representing of 300 m on the ground. Twenty of the points fell in areas disturbed by logging or in non-forested areas (i.e., areas outside old-growth forest) and were eliminated from the sample. The approximate location of each of the remaining eighty points was determined in the field and identified as a general area for sampling. The specific location of a sample stand was guided by the criterion of stand homogeneity. The homogeneity of a sample stand was judged by assessing the uniformity of both vegetation



structure and species dominance (Westhoff and van der Maarel 1978). The intent behind the selection of homogenous stands was not to interject a pre-conceived notion of vegetation types into the sampling scheme, but rather to assure that parameters recorded for a stand were representative of those in the surrounding sample area. For example, vegetation in stream channels, on recent landslides, or under singular gaps in the canopy was, in some cases, obviously atypical of surrounding vegetation and was therefore excluded when positioning the boundaries of the sample stand. The size of the 15 × 25 m (375 m<sup>2</sup>) sample stands was in accordance with empirical values for minimal area in forest vegetation (Mueller-Dombois and Ellenberg 1974).

Every vascular plant species occurring within stand boundaries was identified (Munz 1968) and recorded in the following life-form/height strata categories: canopy trees greater than 50 m tall, sub-canopy trees greater than 5 m tall, small trees and tall shrubs 2–5 m tall, and low shrubs and herbaceous species less than 2 m tall. The Zurich-Montpellier (ZM) cover/abundance scale (Becking 1957) was used to estimate the cover of each recorded species. Basal area of canopy species was estimated by the Bitterlich method (Grosenbaugh 1952). Elevation, aspect, percentage slope, and slope configuration were measured or described, and the soil profile at the center of each stand was described in terms of color, texture, and depth of horizons.

To improve the efficacy of the data analysis, species with frequencies of less than five percent in the total set of stands were removed from the data set and the cover values for the remaining species were transformed according to a scale devised by van der Maarel (1979). The reduced, transformed data matrix was entered into the computer program TWINSpan (Hill 1979) for two-way indicator species analysis. The program was run with all default options except for the definition of pseudospecies cut-levels which were as follows: level 1 = 1–5% cover, level 2 = 6–25% cover, level 3 = >25% cover. The stand classification on the structured TWINSpan table was interpreted at a division level where the floristic composition of stand groups was consistent with that of plant assemblages repeatedly observed in the field. Stands in typical groups formed at this level were selected to represent the recurrent assemblages, or forest associations, in subsequent steps in the analysis.

Discriminant analysis (Tatsuoka 1970; Williams 1983) was used to accomplish two objectives: 1) to provide a criterion for the selection of equal subsets of typical stands for constancy and fidelity calculations, and 2) to classify “transitional” stands (i.e., stands outside the typical groups formed by TWINSpan). The DISCRIMINANT procedure (Klecka 1975) in the SPSS system of computer programs was used for discriminant analysis. The full set of species



entered into the TWINSpan analysis was too large to use as a set of discriminating variables given the number of typical stands representing the forest associations (Tatsuoka 1970). A smaller number of species variables were selected based on results of analysis of variance tests for differences among the groups of typical stands. A set of discriminant functions based on high F-ratio species was derived to discriminate among the groups of typical stands. The discriminant scores of the stands and the pooled within-groups covariance matrix for the functions were used to derive a classification function for each typical group. All stands were scored on each classification function and the scores were converted to two probabilities of association membership (Klecka 1975). One was the probability of a stand being as distant from the typical group centroid as the stand under consideration. Stands with the highest "distance" probabilities were selected to form equal subsets of typical stands for constancy and fidelity determinations. Constancy was calculated as the species percentage frequency in the subset of typical stands representing a forest association. Fidelity was calculated as the species presence in the subset of typical stands expressed as a percentage of its presence in the total set of sample stands (Becking 1957).

The second set of probabilities derived from the discriminant classification functions indicated the likelihood of each stand being a member of each association. All stands in the sample set, including those identified as transitionals in the TWINSpan analysis, were assigned to the association where this "membership" probability was highest. The forest association membership of each stand was then plotted on the sample grid to reveal the spatial distribution of the final classification. Lines were drawn around groups of adjacent stands within the same association to produce a generalized forest association map of the study area (Lenihan 1986).

The final step in the analysis was an ordination of the sample data to display the results of the TWINSpan classification in a low-dimensional space and to relate the classification to environmental gradients in the study area. Principal components analysis was applied to the reduced, transformed data matrix to obtain trial vectors for final analysis by nonmetric multidimensional scaling (NMDS). Chord distances were computed as the measure of resemblances between stands for the NMDS analysis. Computer programs by Ludwig and Reynolds (1988) were run with default values to perform the ordination. To produce an environmental interpretation of the ordination, stand scores on the first two NMDS axes were compared to values for six different topographic variables using the Kendall rank correlation coefficient. The values of elevation and percentage slope were entered into the analysis as recorded in the field. Slope configuration was coded as an ordinal variable (i.e., one for concave, two for even, and three for convex). The slope position of each



sample stand was calculated as the ratio between the stand elevation above the creek and the ridge elevation above the creek. The aspect in degrees azimuth was transformed into two directional vectors (Kercher and Goldstein 1977). The cosine of the aspect represented the north-south vector, and the sine represented the east-west vector.

## RESULTS

Eighty-three vascular plant species were encountered in the sample stands, and 43 species with frequencies of five percent or more were included in the analysis. The stand classification on the structured TWINSpan table was interpreted at the second division level where three typical groups were formed. The typical groups representing the forest associations of the natural area were comprised of 64 stands out of the total set of 80.

Twenty-one species with high F-ratios were selected to serve as discriminators in two discriminant functions. The two functions accounted for 86 and 14 percent respectively of the total variance of the selected species. Sets of fifteen stands with the highest distance probabilities were selected to represent each of the three forest associations in the constancy and fidelity calculations. Species modal cover-abundance values, constancy, and fidelity in each of the three associations are shown in Table 1. Fidelity values are reported in the fidelity classes described by Becking (1957). Character species are those in fidelity classes III–V. Table 2 shows mean basal area and relative dominance of canopy species by association. The forest associations were named by appending the binomial of a character species with a relatively high modal cover value to the name *Sequoia sempervirens*. The three associations named in this manner are the *Sequoia sempervirens/Blechnum spicant* (*Sequoia/Blechnum*) association, the *Sequoia sempervirens/Mahonia nervosa* (*Sequoia/Mahonia*) association, and the *Sequoia sempervirens/Arbutus menziesii* (*Sequoia/Arbutus*) association.

The distribution of the full set of sample stands in the ordination space formed by the first two NMDS axes is shown in Figure 3. The TWINSpan classification of each stand is also identified in this diagram. The NMDS procedure reached a relatively stable stress value (Kruskal, 1964) of 0.138 after 14 iterations. The two NMDS axes were only weakly correlated, so the unrotated configuration was considered adequate. The Kendall rank coefficients for all comparisons of the NMDS axes and the topographic parameters are shown in Table 3. The results of the ordination analysis indicate that *Sequoia/Blechnum* stands are segregated from *Sequoia/Mahonia* and *Sequoia/Arbutus* stands by their scores on the first NMDS axis which are significantly correlated to elevation, slope position, and slope configuration. The second NMDS axis is significantly correlated to slope



TABLE 1. SYNOPTIC TABLE SHOWING SPECIES CONSTANCY/MODAL COVER/FIDELITY IN SETS OF FIFTEEN STANDS REPRESENTING THE THREE FOREST ASSOCIATIONS OF LITTLE LOST MAN CREEK, CA. Constancy values are percentage frequencies in representative stands. Cover values are from the ZM cover-abundance scale (Becking 1957). Fidelity was calculated as the species presence in representative stands expressed as a percentage of its presence in the total set of eighty stands. Character species are those in fidelity classes III–V (Becking 1957).

| Species                          | <i>Sequoia/<br/>Blechnum</i> | <i>Sequoia/<br/>Mahonia</i> | <i>Sequoia/<br/>Arbutus</i> |
|----------------------------------|------------------------------|-----------------------------|-----------------------------|
| Canopy trees                     |                              |                             |                             |
| <i>Picea sitchensis</i>          | 27/1/V                       | —                           | —                           |
| <i>Tsuga heterophylla</i>        | 47/1/II                      | 47/1/II                     | 20/1/II                     |
| <i>Sequoia sempervirens</i>      | 100/3/II                     | 100/3/II                    | 93/2/II                     |
| <i>Pseudotsuga menziesii</i>     | 67/1/II                      | 93/2/II                     | 100/2/II                    |
| <i>Abies grandis</i>             | —                            | 7/1/V                       | —                           |
| Subcanopy trees                  |                              |                             |                             |
| <i>Lithocarpus densiflora</i>    | 67/2/II                      | 100/3/II                    | 100/4/II                    |
| <i>Arbutus menziesii</i>         | —                            | 20/+/II                     | 67/2/IV                     |
| Small Trees/Tall Shrubs          |                              |                             |                             |
| <i>Rubus spectabilis</i>         | 20/1/V                       | —                           | —                           |
| <i>Menziesia ferruginea</i>      | 27/1/V                       | —                           | —                           |
| <i>Corylus cornuta</i>           | 40/2/V                       | —                           | —                           |
| <i>Rhamnus purshiana</i>         | 80/3/V                       | —                           | —                           |
| <i>Vaccinium parvifolium</i>     | 93/1/III                     | 60/1/II                     | 33/+/II                     |
| <i>Vaccinium ovatum</i>          | 100/1/II                     | 93/3/II                     | 100/4/II                    |
| <i>Rhododendron macrophyllum</i> | 47/1/II                      | 93/2/II                     | 87/4/II                     |
| Low Shrubs/Herbs                 |                              |                             |                             |
| <i>Disporum smithii</i>          | 40/1/V                       | —                           | —                           |
| <i>Athyrium filix-femina</i>     | 40/1/V                       | —                           | —                           |
| <i>Adiantum pedatum</i>          | 20/1/V                       | —                           | —                           |
| <i>Stachys mexicana</i>          | 20/1/V                       | —                           | —                           |
| <i>Adenocaulon bicolor</i>       | 20/1/V                       | —                           | —                           |
| <i>Blechnum spicant</i>          | 80/2/IV                      | 20/1/II                     | —                           |
| <i>Vancouveria hexandra</i>      | 40/1/IV                      | 13/+/II                     | —                           |
| <i>Oxalis oregana</i>            | 100/3/III                    | 67/2/II                     | —                           |
| <i>Polystichum munitum</i>       | 100/5/II                     | 100/2/II                    | 47/1/II                     |
| <i>Trillium ovatum</i>           | 47/1/II                      | 13/+/II                     | 47/1/II                     |
| <i>Disporum hookeri</i>          | 13/+/II                      | 20/1/II                     | 13/1/II                     |
| <i>Gaultheria shallon</i>        | 60/1/II                      | 100/3/II                    | 100/2/II                    |
| <i>Viola sempervirens</i>        | 27/+/II                      | 100/2/II                    | 93/1/II                     |
| <i>Mahonia nervosa</i>           | 33/+/II                      | 92/2/III                    | 13/1/II                     |
| <i>Galium aparine</i>            | 33/1/II                      | 87/1/III                    | 13/1/II                     |
| <i>Trientalis borealis</i>       | 13/+/II                      | 20/1/II                     | 47/1/III                    |
| <i>Festuca subulata</i>          | 7/+/II                       | 53/1/IV                     | —                           |
| <i>Carex hendersonii</i>         | —                            | 7/1/V                       | —                           |
| <i>Actaea rubra</i>              | —                            | 7/+/V                       | —                           |
| <i>Iris douglasiana</i>          | —                            | 40/1/V                      | —                           |
| <i>Hierochloa occidentalis</i>   | —                            | 73/1/V                      | —                           |
| <i>Lathyrus vestitus</i>         | —                            | 33/1/V                      | —                           |
| <i>Whipplea modesta</i>          | —                            | 60/1/IV                     | 13/+/II                     |
| <i>Cardamine integrifolia</i>    | —                            | 47/1/III                    | 33/1/II                     |
| <i>Festuca occidentalis</i>      | —                            | 7/+/II                      | 13/1/III                    |



TABLE 1. CONTINUED.

| Species                          | <i>Sequoia/<br/>Blechnum</i> | <i>Sequoia/<br/>Mahonia</i> | <i>Sequoia/<br/>Arbutus</i> |
|----------------------------------|------------------------------|-----------------------------|-----------------------------|
| <i>Goodyera oblongifolia</i>     | —                            | 40/1/II                     | 53/1/III                    |
| <i>Corallorhiza maculata</i>     | —                            | —                           | 47/1/V                      |
| <i>Pleuricospora fimbriolata</i> | —                            | —                           | 33/1/V                      |
| <i>Pteridium aquilinum</i>       | —                            | —                           | 53/1/V                      |

configuration and the east-west azimuth vector and serves mainly to segregate *Sequoia/Mahonia* from *Sequoia/Arbutus* stands.

The mapped distribution of the forest associations (Lenihan 1986) showed a relatively weak correspondence with the distribution of the soil series as mapped by the California Soil-Vegetation Survey (DeLapp et al. 1961a, b). Comparisons of soil profile descriptions from the groups of typical stands revealed a much stronger correlation between forest associations and soil series. Soils on concave lower slopes at the northern end of the study area where the *Sequoia/Blechnum* association is best developed are generally dark brown to brown clay loams with gleyed subsurface horizons. These are the most Melbourne-like soils in the study area. Soils supporting the *Sequoia/Arbutus* association on convex upper slopes and ridgetops at the southern end of the study area are generally grayish brown to pale brown gravelly loams and clay loams. These are the most Hugo-like soils in the study area. Soils occupied by the *Sequoia/Mahonia* association are generally intermediate in character between the Melbourne and Hugo extremes.

DISCUSSION

*Ecological Relationships.* Processes shaping the composition, structure, and distribution of forest associations in Little Lost Man

TABLE 2. MEAN BASAL AREA (BA) (SQUARE METERS/HECTARE) AND RELATIVE DOMINANCE (RD) (PERCENT) OF CANOPY SPECIES IN THE THREE FOREST ASSOCIATIONS OF LITTLE LOST MAN CREEK, CA. Relative dominance is the species' basal area expressed as a percentage of the total basal area.

| Canopy species               | <i>Sequoia/<br/>Blechnum</i> |    | <i>Sequoia/<br/>Mahonia</i> |    | <i>Sequoia/<br/>Arbutus</i> |    |
|------------------------------|------------------------------|----|-----------------------------|----|-----------------------------|----|
|                              | BA                           | RD | BA                          | RD | BA                          | RD |
| <i>Picea sitchensis</i>      | 2                            | 1  | —                           | —  | —                           | —  |
| <i>Tsuga heterophylla</i>    | 4                            | 3  | 7                           | 5  | 2                           | 3  |
| <i>Sequoia sempervirens</i>  | 126                          | 82 | 84                          | 59 | 39                          | 54 |
| <i>Pseudotsuga menziesii</i> | 22                           | 14 | 52                          | 35 | 31                          | 43 |
| <i>Abies grandis</i>         | —                            | —  | 2                           | 1  | —                           | —  |
| Total basal area             | 154                          |    | 145                         |    | 72                          |    |



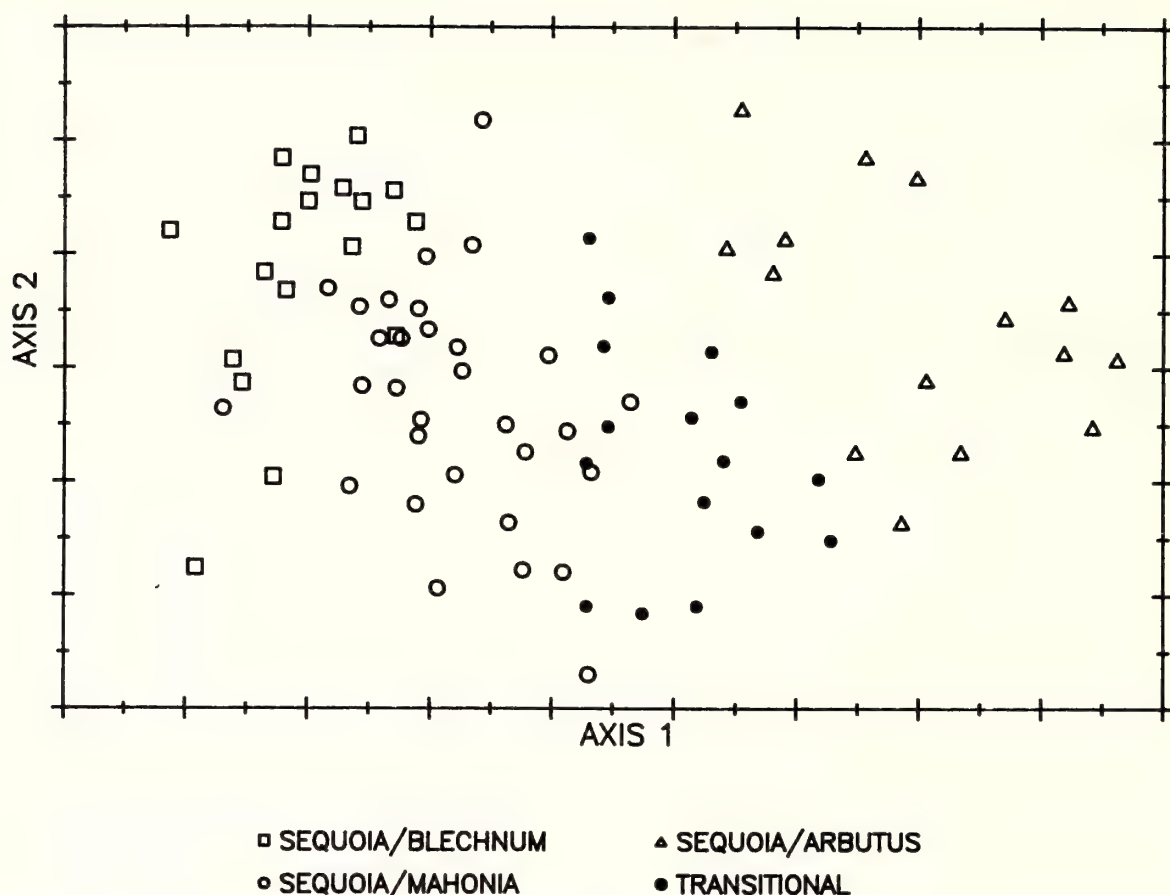


FIG. 3. Ordination diagram showing the distribution of sample stands along the two axes derived by non-metric multidimensional scaling. The TWINSPLAN classification of the stands is also indicated.

Creek can be best understood by viewing the vegetation-environmental complex of the watershed as a hierarchically organized system. From this perspective, the associations are patches comprising the redwood forest at the scale of the watershed, whereas the associations themselves comprise smaller patches generated by disturbance-caused gaps in the canopy (Urban et al. 1987).

The results of the ordination analysis indicate topography at the scale of the watershed is a constraining factor on the distribution of the forest associations. The *Sequoia/Blechnum* association is found at lower elevations and primarily on concave lower slopes, the *Sequoia/Arbutus* association is found at higher elevations on convex upper slopes and ridgetops, and the *Sequoia/Mahonia* association is found at intermediate topographic positions in the watershed. The distribution of the associations along this topographic gradient forms what Barbour et al. (1980) have called a "toposequence."

Topographic pattern at the watershed-level of the scale-hierarchy governs several environmental factors that constrain vegetation development (Spurr and Barnes 1980). These factors include insolation, temperature, soil moisture, and nutrient availability. Sites on concave lower slopes are topographically-shaded, whereas more ex-



TABLE 3. KENDALL RANK CORRELATION COEFFICIENTS FOR STAND SCORES ON NONMETRIC MULTIDIMENSIONAL SCALING AXES AND TOPOGRAPHIC VARIABLES. Asterisks indicate significance level (\*,  $p > 0.05$ ; \*\*,  $p > 0.001$ ).

|                            | Axis 1    | Axis 2    |
|----------------------------|-----------|-----------|
| Stand elevation            | -0.6095** | 0.0335    |
| Slope                      | 0.1457    | -0.1192   |
| Slope position             | -0.2330** | 0.1237    |
| Slope configuration        | -0.3370** | 0.1508*   |
| North-South azimuth vector | 0.1308    | 0.0042    |
| East-West azimuth vector   | -0.0185   | -0.2789** |

posed upper slopes and ridgetops receive more insolation. Cold air drains downslope towards concave lower slopes and away from upper slopes and ridgetops. Soil moisture and nutrient availability are greater on concave lower slopes because evapotranspiration rates are lower in cooler microclimates and water and nutrients are transported downhill towards finer-textured colluvial soils. In Little Lost Man Creek, extremes in microclimate and soil moisture availability along the toposequence are probably accentuated by the higher incidence of summer fog at lower elevations in the watershed (Harris 1987).

Natural disturbance is also controlled indirectly by topographic pattern at the watershed-scale (White 1979). Fire, mass movements, and windfall are the likely sources of gap-producing disturbance in the research natural area. The local intensity, frequency, and areal extent of fire are controlled by several interacting factors related to topography including the frequency of ignition sources and the moisture content and structural characteristics of fuels (Martin 1982). On exposed upper slopes and ridgetops, lightning strikes are more frequent and fuels are drier. In the study area, the dense, woody structure of the subcanopy and small tree/tall shrub strata in the *Sequoia/Arbutus* association creates a relatively continuous fuel structure at these topographic positions. In contrast, on lower concave slopes, natural sources of ignition are less frequent and the moisture content of fuels is greater given cooler microclimates and moister soils. Also on lower slopes in the study area, the poorly-developed subcanopy and small tree/tall shrub strata in the *Sequoia/Blechnum* association creates relatively discontinuous fuels. Thus it is likely that fire regimes at the watershed-scale of the study area are spatially-patterned along topographic gradients and may vary from relatively large crown fires on convex upper slopes and ridgetops to smaller, less frequent surface fires on concave lower slopes. This hypothesis is supported by the results of the very few coast redwood fire history studies that have been conducted in the northern portion of the species' range (Becking 1967; Veirs 1982).



The spatial patterning of mass movement and windfall are related to watershed-scale topography as well. In Little Lost Man Creek, conditions triggering deep-seated soil creep and slump-earthflow (i.e., steep slopes and deep, fine-textured soils with low cohesion) (Coleman 1973) occur almost exclusively on lower concave slopes, and thus gap-producing mass-movement is probably restricted to these sites. The spatial patterning of windthrow is more difficult to predict. The instability of soils reduces the windfirmness of trees on lower concave slopes, but shallower soils and greater exposure to wind probably result in more frequent and extensive blowdown on upper slopes and ridgetops.

In the context of watershed-level constraints on vegetation development, how do gap-level processes determine the structure and composition of the forest associations in the research natural area? Although gap-level processes are recognized as a primary force shaping tall coniferous forests throughout the Pacific Northwest (Stewart 1986, 1988, 1989; Spies and Franklin 1989; Taylor 1990), gap characteristics and vegetation response in coast redwood forests are, to date, largely unknown. Nevertheless, given some assumptions as to the size and frequency of gaps produced by different types of disturbance, and given what is known about ecological tolerances of important species in the study area, one can propose gap-level, mechanistic hypotheses to account for the structure and composition of vegetation observed at the association-level of the hierarchy.

For example, a typical windfall or slope failure probably creates a relatively small gap in the *Sequoia/Blechnum* canopy compared to that produced by windfall or fire in the *Sequoia/Arbutus* type. A small gap on a concave lower slope deep in the Little Lost Man Creek canyon would not admit much light, and consequently, tree seedling establishment would be largely restricted to shade-tolerant species. Windfall and slope failure disrupt soil horizons and expose mineral soil at the surface, and the very tolerant *Sequoia* is favored by a moist, mineral bed for seed germination and seedling establishment (Florence 1964; Fowells 1965). Seedlings of the tolerant *Picea sitchensis* and *Tsuga heterophylla* could also become established under gaps in the *Sequoia/Blechnum* canopy, but the superior height growth and longevity of *Sequoia* on moist, shaded, nutrient-rich sites probably account for its eventual dominance in the developing canopy (Fowells 1965). Infrequent surface fires in the *Sequoia/Blechnum* association would also encourage *Sequoia* dominance in the canopy. *Sequoia* forms lignotubers at a very young age and even seedlings sprout after damage by fire (Roy 1966), whereas *Picea* and *Tsuga* are non-sprouting species. At later stages in gap-development, the thick, fibrous bark of *Sequoia* would afford the species an even greater resistance to fire than its thin-barked, shade-tolerant associates (Fowells 1965).



The scattered occurrence of *Pseudotsuga menziesii* as large, isolated individuals attests to the infrequent establishment and persistence of this relatively intolerant species (Fowells 1965) in the *Sequoia/Blechnum* type. In old-growth redwood stands near the research natural area, Veirs (1982) related *Pseudotsuga* establishment on moist lower slopes to the occurrence of canopy-disrupting fire with a return interval of greater than 500 yr. Presumably windthrow or slope failure on lower slopes in the watershed could also occasionally produce a gap large enough to provide both sufficient light penetration and the mineral soil bed (Sudworth 1967) necessary for *Pseudotsuga* germination and establishment. Regardless of the initial mechanism, once *Pseudotsuga* is established in a gap in the *Sequoia/Blechnum* canopy, the thick furrowed bark of a mature individual would promote its persistence under the normal regime of light surface fires (Fowells 1965).

The deep shade cast by the dense *Sequoia* canopy in a mature gap probably accounts for the poor development of the subcanopy and small tree/tall shrub strata in the *Sequoia/Blechnum* type. There is apparently insufficient photosynthetic energy available to maintain a dense, woody structure in the understory (Whittaker 1975; Stewart 1988). Several small trees and tall shrubs characterize this association, but they are found only in small clumps at scattered locations. The floristic composition of the low shrub/herb stratum is a further indication of low light availability in the understory. The ferns and other herbaceous plants that characterize the *Sequoia/Blechnum* type are indicative of both low light and high moisture regimes in old-growth redwood forests (Waring and Major 1964).

At the opposite end of the toposequence, crown fires and blow-down on upper slopes and ridgetops presumably create relatively large gaps in the canopy of the *Sequoia/Arbutus* type and promote the mixture of shade intolerant and sprouting species that characterize the upper strata in this association. The high percentage of sprouting species indicates the importance of fire in this type. Five of seven woody plants comprising the bulk of the canopy, subcanopy, and small tree/tall shrub strata are capable of sprouting from lignotubers or roots. After a destructive crown fire opened a large gap in the *Sequoia/Arbutus* type, the burl tissue of *Sequoia*, *Lithocarpus densiflora*, and *Arbutus menziesii* could quickly regenerate the canopy and subcanopy in the gap while the sprouting root crowns of *Rhododendron macrophyllum* and *Vaccinium ovatum* re-established the small tree/tall shrub stratum.

Severe fires which open up the canopy and expose mineral soils would favor the germination and establishment of the shade-intolerant *Pseudotsuga* (Franklin and Dyrness 1973) which eventually attains co-dominance with *Sequoia* in the canopy of *Sequoia/Arbutus* stands. *Pseudotsuga* apparently also becomes established in light



spots under a mature canopy/subcanopy as clumps of saplings were often observed in the understory of this association. A small gap in the canopy created by windfall would afford these young trees an opportunity to reach a position in the canopy.

The third old-growth forest association in the research natural area, the *Sequoia/Mahonia* type, occupies intermediate positions along the toposequence. At lower elevations where summer fog occurs with more frequency, the association occupies exposed convex positions on ridgetops and upper slopes where soils are often shallow and gravelly. At higher elevations, the type occupies relatively cool east-facing sites adjacent to the main stem of the creek, especially concave positions where soils are deeper and finer-textured. Wind-throw, slope failure, and relatively infrequent crown fire could all be gap-producing mechanisms given the varied topographic positions occupied by this association.

The structure and composition of the *Sequoia/Mahonia* association are likely a product of the relatively mesic nature of sites occupied by this type and perhaps also of an intermediate disturbance regime compared to those at the two extremes of the toposequence. Dominance in the canopy of the *Sequoia/Mahonia* association is shared by *Sequoia* and *Pseudotsuga* as in the xeric type, but the total basal area of these canopy species is nearly as large as that in the moist type. The subcanopy and small tree/tall shrub strata are better developed in contrast to the poor development of these strata in the moist type but are less dense than those in the xeric association. The structure and composition of these strata suggest a relatively mesic moisture regime and perhaps a transitional fire regime between the light surface fires and more destructive crown fires at the moist and xeric ends of the toposequence.

The low shrub/herb stratum in the *Sequoia/Mahonia* association is the most diverse in the study area. Dominant species in this layer include species common in both the moist type (i.e., *Polystichum munitum* and *Oxalis oregana*) and the xeric type (i.e., *Gaultheria shallon* and *Viola sempervirens*). The co-dominance of moist and xeric components in the low shrub/herb stratum is another indication of the mesic status of the *Sequoia/Mahonia* type. Furthermore, the characteristic herbaceous species *Iris douglasiana*, *Hierochloa occidentalis*, and *Whipplea modesta* are indicative of intermediate moisture and light regimes in old-growth redwood forests (Waring and Major 1964).

*Symmetry of Pattern and Process Across Scale.* According to the principles of hierarchy theory, interlevel relationships in a hierarchical structure are established by choosing a phenomenon of interest at a given level and examining that phenomenon at the next higher and/or lower levels. Movement from one level to the next is accomplished by changing the grain and/or extent of the observation set.



If the phenomenon is of interest at both higher and lower levels then a linkage between levels is warranted (Allen et al. 1984).

The gradient in vegetation structure and composition along the toposequence formed by the forest associations is a marked feature of vegetation pattern at the watershed-level of the hierarchy. At the lower end of the toposequence, *Sequoia* dominates a single-layer canopy and development of the small tree/tall shrub is poor. At the upper end, the two-layered overstory is composed of *Sequoia*, *Pseudotsuga*, and hardwoods, and the small tree/tall shrub layer is more fully-developed. Recurrence of this gradient at the finer scale of the forest association and coarser scale of the redwood region would corroborate linkage across three adjacent levels of the hierarchy.

To examine vegetation pattern above and below the watershed-level of the hierarchy, a change in the grain and/or extent of the observation set is required. The observation set for the watershed-level analysis is the three groups of typical stands formed at the second division-level in the TWINSPAN analysis. To examine pattern at the level below the watershed-level (i.e., at the level of individual associations), an increase in grain and decrease in extent were obtained by examining the fine-structure of each representative group of stands at the third-division level in the TWINSPAN analysis.

The fine-structure of the *Sequoia/Blechnum* group of stands shows a relationship between clumps of woody understory plants and the presence of *Pseudotsuga* suggestive of relatively immature patches in the matrix of this lower slope type. A small group of stands within the *Sequoia/Arbutus* group, distinguished by the reduced importance of *Pseudotsuga* and a relatively sparse hardwood subcanopy, suggests patches of relatively long-term forest development in a more frequently disturbed forest matrix on upper slopes and ridgetops. Apparently, there is a structural/compositional gradient related to patch (or gap) development at the association-level; a gradient comparable to that observed along the toposequence at the watershed-level of the hierarchy.

To examine vegetation pattern at the level above the watershed-level (i.e., at the regional-level), a decrease in the grain and increase in the extent of the observation set was obtained by considering the results of this study as a single datum in the set of all the watershed-level vegetation studies in the redwood forest region. Several authors (Becking 1967, 1971; Dyrness et al. 1973; McBride and Jacobs 1978; Greenlee 1983; Borchert et al. 1988) have described the structure and composition of redwood forests at scales comparable to the watershed-level at various locations throughout the range of *Sequoia*. Taken together, these descriptions and the results of this study reveal a gradient from *Sequoia* dominance to a greater importance of *Pseudotsuga* and hardwoods in mesic stands along a north-south axis though the entire redwood forest region. This gradient is also evident



in the regional-scale analysis of Zinke (1977) and Kuchler's (1977) vegetation map of California. Once again, vegetation pattern links two levels in the redwood hierarchy, in this case, those of the region and the watershed.

The underlying environmental and disturbance gradients shaping the redwood forest at the regional scale may also be comparable to those at the scale of the watershed. I have calculated monthly values of potential and actual evapotranspiration (Thornthwaite and Mather 1957) for several weather stations (U.S. Dept. of Commerce 1964) throughout the range of *Sequoia*, and results indicate a definite moisture gradient along the north-south axis of the redwood forest region. Walter et al.'s (1975) climate diagrams for coastal California illustrate the same point. Towards the south, annual water deficits are larger and the deficit period commences earlier in the year. The shift from *Sequoia* dominance to a greater importance of *Pseudotsuga* and hardwoods is also accompanied by a shift in fire regimes at the regional scale (Veirs 1985). Fire-return intervals on relatively mesic sites vary from 250–500 years in the northern part of *Sequoia*'s range (Veirs 1982) to 20–50 yr in more southerly locations (Fritz 1931; Greenlee 1983; Jacobs et al. 1985; Stuart 1987).

The gradient in vegetation structure and composition formed by the forest associations along the toposequence in the Little Lost Man Creek watershed resembles both a scaled-down version of the regional-level pattern and a scaled-up version of the gap mosaic at the association-level. This symmetry across scales indicates redwood vegetation exhibits the self-similarity of a scaling fractal (Mandelbrot 1983). Proof of this assertion would involve determining the fractal dimension of vegetation at each of the three different levels of the hierarchy. This, in turn, would require both fine-grained and extensive sampling throughout the redwood region. An analysis of the fractal dimensions of redwood vegetation would be worthwhile not only from a purely theoretical standpoint, but also as aid in the design of statistically-valid sampling schemes (Palmer 1988) for ecological research in coastal redwood forests.

#### ACKNOWLEDGMENTS

I am most grateful to Redwood National Park for providing financial support for this research and to Stephen Veirs, Jr., for suggesting this topic. Robert Frenkel and Robert DeVelice provided helpful comments on an earlier version of this paper. I also acknowledge the constructive comments of Richard Pimental and an anonymous reviewer. Finally, I am indebted to Rudolph Becking for sharing his extensive knowledge of coastal redwood phytosociology.

#### LITERATURE CITED

- ALLEN, T. F. H. and T. B. STARR. 1982. Hierarchy: perspectives for ecological complexity. Univ. Chicago Press, Chicago. 326 pp.  
———, T. W. HOEKSTRA, and R. V. O'NEILL. 1984. Interlevel relations in ecological



- research and management: some working principles from hierarchy theory. USDA For. Serv. Gen. Tech. Rep. RM-110. Rocky Mountain For. and Range Exp. Sta. Fort Collins, CO. 11 pp.
- BARBOUR, M. G., J. H. BURKE, and W. D. PITTS. 1980. Terrestrial plant ecology. Benjamin/Cummings Publ. Co., Menlo Park, CA. 604 pp.
- BECKING, R. W. 1957. The Zurich-Montpellier School of Phytosociology. Bot. Rev. 23:411-488.
- . 1967. The ecology of the coastal redwood forest and the impact of the 1964 floods upon redwood vegetation. Final report. NSF Grant GB No. 3468. 91 pp. (on file at Humboldt State Univ. library, Arcata, CA).
- . 1971. The ecology of the coastal redwood forests of northern California and the impact of the 1964 flood upon redwood vegetation. Final Report. NSF Grant GB No. 6310. 158 pp. (on file at Humboldt State Univ. library, Arcata, CA).
- BORCHERT, M., D. SEGOTTA, and M. D. PURSER. 1988. Coast redwood ecological types of southern Monterey County, California. U.S.D.A. For. Serv. Gen. Tech. Rep. PSW-107. Pacific Southwest For. and Range Exp. Sta. Berkeley, CA. 27 pp.
- CALIFORNIA DEPARTMENT OF WATER RESOURCES. 1965. Land and water use in the Redwood Creek Hydrographic Unit. Bull. 94-7. Sacramento. 80 pp.
- COLEMAN, R. J. 1973. The history of mass-wasting processes in the lower Redwood Creek basin, Humboldt County, California. M.S. thesis. Pennsylvania State Univ., University Station. 120 pp.
- DELAPP, J. A., and B. F. SMITH. 1977. Tables for the soil-vegetation map of the NE  $\frac{1}{4}$  of Orick quadrangle (10A-1). U.S.D.A. For. Serv., Pacific Southwest For. and Range Exp. Sta. Berkeley, CA. 5 pp.
- , R. SKOLMAN, and B. SMITH. 1961a. Timber stand and vegetation cover map, soil-vegetation map, legends and interpretation—SE  $\frac{1}{4}$  of Orick quadrangle (10A4). California Cooperative Soil-Vegetation Survey. U.S.D.A. For. Serv., Pacific Southwest For. and Range Exp. Sta. Berkeley, CA. 40 pp.
- , ———, and ———. 1961b. Timber stand and vegetation cover map, soil-vegetation map, legends and interpretation—SW  $\frac{1}{4}$  of Tectah Creek quadrangle (11B3). California Cooperative Soil-Vegetation Survey. U.S.D.A. For. Serv. Pacific Southwest For. and Range Exp. Sta. Berkeley, California. 37 pp.
- DYRNESS, C. T., J. F. FRANKLIN, and C. MASER. 1973. Wheeler Creek Research Natural Area. Supplement No. 1 to Federal Research Natural Areas in Oregon and Washington: a guidebook for scientists and educators. U.S.D.A. For. Serv., Pacific Northwest For. and Range Exp. Sta. Portland, OR. 16 pp.
- ELFORD, C. R. and M. R. McDONOUGH. 1974. The climate of Humboldt and Del Norte counties. Humboldt and Del Norte Counties Agri. Ext. Serv. Univ. California. Berkeley. 52 pp.
- FLORENCE, R. G. 1964. Decline of old-growth redwood forests in relation to some soil microbiological processes. Ecology 46:52-64.
- FOWELLS, H. A. 1965. Silvics of the forest trees of the United States. Agricultural Handbook No. 271. U.S. Department of Agriculture. Washington, D.C. 762 pp.
- FRANKLIN, J. F. and C. T. DYRNESS. 1973. Natural vegetation of Oregon and Washington. U.S.D.A. For. Serv. Gen. Tech. Rep. PNW-8. Pacific Northwest For. and Range Exp. Sta. Portland, OR. 417 pp.
- FREEMAN, G. J. 1971. Summer fog drip in the coastal redwood forest. M.S. thesis, Humboldt State Univ. Arcata, CA. 100 pp.
- FRITZ, E. 1931. The role of fire in the redwood region. J. Forestry (Washington) 29:939-950.
- GREENLEE, J. M. 1983. Vegetation, fire history, and fire potential of Big Basin Redwoods State Park, California. Ph.D. dissertation. Univ. California, Santa Cruz.
- GROSENBAUGH, L. R. 1952. Plotless timber estimates: new, fast, easy. J. Forestry (Washington) 50:32-37.



- HARRIS, S. A. 1987. Relationship of convection fog to characteristics of the vegetation of Redwood National Park. M.S. thesis. Humboldt State Univ., Arcata, CA. 60 pp.
- HILL, M. O. 1979. TWINSpan: a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and the attributes. Section of Ecology and Systematics, Cornell Univ. Ithaca, NY. 90 pp.
- IRWIN, W. P. 1960. Geologic reconnaissance of the northern Coast Ranges and Klamath Mountains, California, with a summary of mineral resources. Bull. 179. Calif. Div. Mines and Geol. San Francisco. 507 pp.
- JACOBS, D. F., D. W. COLE, and J. MCBRIDE. 1985. Fire history and perpetuation of natural coast redwood ecosystems. *J. Forestry* (Washington) 83:494–497.
- KERCHER, J. R. and R. A. GOLDSTEIN. 1977. Analysis of an eastern Tennessee oak hickory forest by canonical correlation of species and environmental parameters. *Vegetatio* 35:153–163.
- KLECKA, W. R. 1975. Discriminant analysis. Pp. 434–467 in N. H. Nie (ed.), *SPSS: statistical package for the social sciences*. McGraw-Hill Book Company, New York. 675 pp.
- KRUSKAL, J. B. 1964. Nonmetric multidimensional scaling: a numerical method. *Psychometrika* 29:115–129.
- KUCHLER, A. W. 1977. Appendix: the map of the natural vegetation of California. Pp. 909–938 + map in M. G. Barbour and J. Major (eds.), *Terrestrial vegetation of California*. John Wiley and Sons Publishers, New York. 1002 pp.
- LENIHAN, J. M. 1986. The forest associations of the Little Lost Man Creek Research Natural Area, Redwood National Park, CA. M.S. thesis. Humboldt State Univ., Arcata, CA. 85 pp.
- LUDWIG, J. A. and J. F. REYNOLDS. 1988. *Statistical ecology: a primer on methods and computing*. John Wiley and Sons, New York. 337 pp. + computer program diskette.
- MAAREL, E. VAN DER. 1979. Transformation of cover-abundance values in phytosociology and its effect on community similarity. *Vegetatio* 39:97–114.
- MANDELBROT, B. 1983. *The fractal geometry of nature*. W. H. Freeman and Co., New York. 468 pp.
- MARTIN, R. E. 1982. Fire history and its role in succession. Pp. 92–99 in J. E. Means (ed.), *Forest succession and stand development in the Pacific Northwest*. Proc. of 1981 Symposium at Oregon State Univ. Forest Research Laboratory, Corvallis, OR. 170 pp.
- MCBRIDE, J. and D. JACOBS. 1978. Vegetation history of Muir Woods National Monument. Final Rep. Natl. Park Serv. Contract No. CX 8000-6-0035. Dept. For. and Cons., Univ. California. Berkeley. 39 pp.
- MUELLER-DOMBOIS, D. and H. ELLENBERG. 1974. *Aims and methods of vegetation ecology*. John Wiley and Sons Publishers, New York. 547 pp.
- MUNZ, P. A. 1968. *A California flora and supplement*. University of California Press, Berkeley. 1681 + 224 pp.
- O'NEILL, R. V., D. L. DEANGELIS, J. B. WAIDE, and T. F. H. ALLEN. 1986. A hierarchical concept of the ecosystem. Princeton Univ. Press, Princeton, NJ.
- PALMER, M. W. 1988. Fractal geometry: a tool for describing spatial patterns of plant communities. *Vegetatio* 75:91–102.
- ROY, D. F. 1966. Silvical characteristics of redwood. U.S.D.A. Forest Service Research Paper PSW-28. Pacific Southwest Forest and Experimental Station. Berkeley, CA. 20 pp.
- SPIES, T. A. and J. F. FRANKLIN. 1989. Gap characteristics and vegetation response in coniferous forests of the Pacific Northwest. *Ecology* 70:543–545.
- SPURR, S. H. and B. V. BARNES. 1980. *Forest ecology*. John Wiley and Sons Publishers, New York. 687 pp.
- STEWART, G. H. 1986. Population dynamics of a montane conifer forest, Western Cascade Range, Oregon, USA. *Ecology* 67:534–544.



- . 1988. The influence of canopy cover on understorey development in forests of the western Cascade Range, Oregon, USA. *Vegetatio* 76:79–88.
- . 1989. The dynamics of old-growth *Pseudotsuga* forests in the western Cascade Range, Oregon, USA. *Vegetatio* 82:79–94.
- STUART, J. D. 1987. Fire history of an old-growth forest of *Sequoia sempervirens* (Taxodiaceae) forest in Humboldt Redwoods State Park, California. *Madroño* 34:128–141.
- SUDWORTH, G. B. 1967. Forest trees of the Pacific Slope. Dover Publications, Inc. New York. 455 pp. (reprint of 1900 edition).
- TATSUOKA, M. M. 1970. Selected topics in advanced statistics No. 6.: discriminant analysis. Institute for Personality and Ability Testing, Campaign, IL. 57 pp.
- TAYLOR, A. H. 1990. Disturbance and persistence of Sitka spruce (*Picea sitchensis*) in coastal forests of the Pacific Northwest. *J. Biogeog.* (in press).
- THORNTHWAITE, C. W. and J. R. MATHER. 1957. Instructions and tables for computing potential evapotranspiration and the water balance. *Publ. Climato.* 10: 185–311.
- URBAN, D. L., R. V. O'NEILL, and H. H. SHUGART, JR. 1987. Landscape ecology: a hierarchical perspective can help scientists understand spatial patterns. *Bio-Science* 37:119–127.
- U.S. DEPARTMENT OF COMMERCE. 1964. Climatography of the United States No. 86-4 (California). Decennial census and climatic summary. Supplement for 1951–1960. Washington, D.C.
- VEIRS, S. D., JR. 1982. Coast redwood forest: stand dynamics, successional status, and the role of fire. Pp. 119–141 in J. Means (ed.), *Forest succession and stand development in the Pacific Northwest. Proceedings of the 1981 Symposium at Oregon State University. Forest Research Laboratory, Corvallis, OR.* 170 pp.
- (ed.). 1985. Coastal redwood fire ecology and prescribed fire management: proceedings of a workshop held October 15–16, 1984 in Arcata, CA. Cooperative Park Studies Unit, Redwood National Park, Arcata. 125 pp.
- WALTER, H., E. HARNICKELL, and D. MUELLER-DOMBOIS. 1975. Climate-diagram maps of the individual continents and the ecological climatic regions of the earth: map 1, North America. Springer-Verlag Publishers, New York. 36 pp. + 9 maps.
- WARING, R. M. and J. MAJOR. 1964. Some vegetation of the California coastal redwood region in relation to gradients of moisture, nutrients, light, and temperature. *Ecol. Monogr.* 34:167–215.
- WESTHOFF, V. and E. VAN DER MAAREL. 1978. The Braun-Blanquet approach. Pp. 287–399 in R. H. Whittaker (ed.), *Classification of plant communities.* Dr. W. Junk Publishers, The Hague, The Netherlands. 408 pp.
- WHITE, P. S. 1979. Pattern, process, and natural disturbance in vegetation. *Bot. Rev.* 45:229–299.
- WHITTAKER, R. H. 1975. *Communities and ecosystems.* 2nd ed. Macmillan Publishing Co., New York.
- WILLIAMS, B. K. 1983. Some observations on the use of discriminant analysis in ecology. *Ecology* 64:1283–1291.
- ZINKE, P. J. 1977. The redwood forest and associated north coast forests. Pp. 679–698 in M. G. Barbour and J. Major (eds.), *Terrestrial vegetation of California.* John Wiley and Sons Publishers, New York. 1002 pp.

(Received 15 Mar 1989; revision accepted 4 Jan 1990.)



# FOREST HABITAT TYPES OF THE SOUTH WARNER MOUNTAINS, MODOC COUNTY, CALIFORNIA

GREGG M. RIEGEL  
U.S.D.A Agricultural Research Service,  
920 Valley Road,  
Reno, NV 89512

DALE A. THORNBURGH  
Department of Forestry, Humboldt State University,  
Arcata, CA 95521

JOHN O. SAWYER  
Department of Biology, Humboldt State University,  
Arcata, CA 95521

## ABSTRACT

We describe the forest habitat types of the South Warner Mountains in northeastern California using floristic composition and associated environmental variables from 261 relevés. Floristic data were analyzed with an agglomerative polythetic hierarchical cluster analysis. Results indicate four series (*Cercocarpus ledifolius*, *Populus tremuloides*, *Abies concolor*, and *Pinus albicaulis*), containing nine habitat types and two phases. Environmental variables (elevation, aspect, slope, surface rock cover, and topographical position) were ordinated with principal component analysis and a moisture equivalency index. These results indicate that forest habitat types occur along a complex elevation/soil/moisture gradient. The elevation, aspect, and topographic position were the best predictors of general pattern. Only distribution of *Cercocarpus ledifolius* and *Populus tremuloides* series appear to be edaphically controlled.

The montane and subalpine conifer forests of the Warner Mountains in northeastern California are of interest because of their isolation from Sierra Nevada and Cascade Range mountains by the expanses of the Modoc plateau and surrounding deserts (Rundel et al. 1977; Vasek and Thorne 1977). The patchy *Pinus jeffreyi* and *Abies concolor* forests are considered depauperate examples of Sierra Nevada and southern Cascade Range forests (Critchfield and Allenbaugh 1969). Griffin and Critchfield (1972) noted the absence of four montane and subalpine conifers from the Warner Mountains, two that are typically Sierran, *Abies magnifica* and *Pinus lambertiana*, and two that occur in the Pacific Northwest and Sierra Nevada-Cascade Range, *Pseudotsuga menziesii* and *Tsuga mertensiana*. Other investigators have briefly discussed forests that do occur in the Warner Mountains: *Pinus jeffreyi*, *P. ponderosa*, and *P. washo-*



*ensis* forests (Haller 1961, 1965; Pease 1965; Critchfield 1984); *Populus tremuloides* and *Pinus contorta* ssp. *murryana* forests (Vale 1977; Winkler and Dana 1977); and subalpine *P. albicaulis* stands (Critchfield and Allenbaugh 1969; Vale 1977). Classification of forest and range vegetation has been performed in much of the Pacific Northwest and parts of the interior West (e.g., Franklin and Dyrness 1973; Pfister et al. 1977). Pfister and Arno (1980) define habitat type as land areas potentially capable of producing similar climax communities. Mature or near "climax" communities can be identified by the dominant composition of the understory. Since the establishment and development of plants are governed by the environment, specific responses can be expected for an equivalent set of environmental conditions (Daubenmire 1968).

The lack of a habitat type classification in northeastern California and the relatively undisturbed vegetation led us to choose the forests within the South Warner Wilderness Area for our study. Our objective was to describe the habitat types for the forests of the area.

### STUDY AREA

We define the South Warner Mountains as the portion of the range south of Cedar Pass (Calif. State Highway 299), and the North Warner Mountains as the portion which is north. The South Warner Wilderness Area of the Modoc National Forest is located between 41°14' and 41°30'N latitude and 120°07' and 120°17'W longitude, in the South Warner Mountains of Modoc Co. in the extreme northeastern corner of California. The area encompasses approximately 28,647 ha and averages about 11 km in width and 26 km in length. The Wilderness Area encompasses elevations from 1457 to 3016 m.

Climate is considered continental (Pease 1965). Mean annual precipitation in Jess Valley (1555 m), which is adjacent to the west central portion of the study area, is 454 mm (State of Calif. 1980). The snow pack averages 1077 mm in depth and contains an equivalent 404 mm of water (State of Calif. 1981). Average temperatures in Alturas (1334 m) located 25 km from the study area range from -2.2°C in January to 19.1°C in July (U.S.D.C. Weather Bureau 1970).

The Warner Mountains are part of the western edge of the Great Basin Province. Structurally the range is characteristic of the Great Basin; however, the rocks are compositionally related to the Modoc Plateau (Macdonald and Gay 1966). In general, the rock sequences comprising the Warner Mountains are Miocene volcanic rocks overlying Oligocene sedimentary rocks (Duffield and Weldin 1976). The volcanic rocks consist of rhyolitic ash-flow tuff, andesite flows, rhyolitic to andesitic air-fall pyroclastic deposits, basalt flows or small



local rhyolite flows. The sedimentary rocks consist of bedded siltstone and sandstone.

Soils in the study area are classified primarily as mollisols with some alfisols and entisols (Luckow 1986).

Some authorities view the flora of the Warner Mountains to be Sierran (Cronquist et al. 1972; Munz 1973), whereas others consider it more Great Basin or intermountain in character (Raven 1977; Harper et al. 1978; Raven and Axelrod 1978; Reveal 1979). Major and Taylor (1977) have suggested that the presence of Rocky Mountain alpine species found here indicates a floristic, and therefore a probable vegetational, relationship to the east.

Local weather is strongly influenced by the orographic effect of the crest of the South Warner Mountains. The gentle west slope ( $\bar{x} = 10^\circ$ ) receives a greater amount of precipitation than the steeper east slope ( $\bar{x} = 25^\circ$ ), producing extensive forests within a mosaic of sagebrush-steppe and meadows. Vegetation on the east slope is dominated by sagebrush (*Artemisia tridentata*) with scattered forests and meadows associated with drainages and seeps. This general lack of forest may also relate to steep, rocky scarp topography on the east side. Extensive areas of juniper (*Juniperus occidentalis* ssp. *occidentalis*) and sagebrush occur on the lower slopes on both the east and west sides.

The Warner Mountains have served as summer range for livestock since the late 1860's. By 1900, 60,000 sheep and 40,000 cattle were using the Warner Mountains (Pease 1965). In 1904 overgrazing pressures stimulated the formation of a federal reserve to manage the Warner Mountains. The U.S. Forest Service established a primitive area in 1931 which is now the South Warner Wilderness Area. Currently 3000 sheep [1070 AUM's (AUM = animal unit month; cow and calf feed requirement, or equivalent, for one month)] and 120 cattle (396 AUM's) graze in the Wilderness. An additional 402 cattle (1378 AUM's) are on allotments that are partially within the Wilderness boundaries.

## METHODS

*Data collection.* Initial reconnaissance occurred in 1978. Sampling was conducted throughout the summers of 1978, 1979, and 1980, with field verification during 1981 and 1983. We did not sample areas with evidence of heavy cattle or sheep grazing (e.g., manure, defoliated plants, and dust wallows). Fire evidence was noted.

Approximately 95% of the forests grow on volcanic soils. Vegetation occurring on sedimentary soil, which typically is conifer woodlands, and the juniper-sagebrush woodlands that occur on the lower slopes of the east side were not sampled. However, undisturbed vegetation outside the wilderness boundary was also examined during the reconnaissance.



Methods were adapted from Mueller-Dombois and Ellenberg (1974), Gauch (1982), and Riegel (1982). Reconnaissance suggested four types of frequently occurring floristic assemblages and associated habitats. Each type was sampled throughout its extent using relevés (Mueller-Dombois and Ellenberg 1974). Sampling was confined to sites possessing a reproducing overstory with consistent aspect and slope. Relevés ranged in size from 8 m<sup>2</sup> to 2000 m<sup>2</sup>.

Vascular plant species were censused in the relevé, and each was evaluated in terms of cover and relative abundance using a modified Braun-Blanquet scale (Mueller-Dombois and Ellenberg 1974). Average heights of the tree and shrub layers were measured. Diameter at breast height (DBH = 1.37 m) and basal area of trees were measured. Elevation, aspect, slope, topographic position, soil surface texture, surface rock cover, and forest floor depth were measured (Riegel 1982).

A total of 261 relevés contained information of 211 species. Relevé location was recorded on topographic maps deposited in the Archives of Humboldt State University library. Voucher specimens of collected plants are deposited in the Humboldt State University Herbarium (HSC) (Riegel and Schoolcraft 1990). Nomenclature follows Munz (1973).

*Data analysis.* Agglomerative polythetic hierarchical cluster analysis was used to gain an initial understanding of the structure in the data (Gauch 1982). Relevés were compared using a modified version of Orloci's (1967) similarity coefficient, Euclidean distance (Gauch 1982), and Ward's method (Ward 1963), utilizing error sum of squares. Ward's method was chosen as the cluster technique to create the dendrogram (Riegel 1982). Thirty-five species were very rare and were deleted from the analysis. A summary table was constructed using the groups defined from the interpretation of the dendrogram (Mueller-Dombois and Ellenberg 1974; Gauch 1982) (Table 1).

The classification framework follows Pfister and Arno (1980) using, in increasing order of resolution, 1) *Series* (exhibits major environmental differences reflected by tree distribution and is named for the potentially climax-dominant tree); 2) *Habitat type* (reflects differences in the environment by vegetation composition and is named by the series and characteristic understory species); 3) *Phase* (represents minor environmental differences within a habitat and is named by an indicator species).

Environmental relationships among the groups at both the series and habitat type levels were examined using both direct and indirect gradient analyses. A direct gradient analysis, used elevation, aspect, and topographic position to rate the soil moisture equivalence for each relevé (Sawyer 1975). An indirect technique, principal component analysis was used to derive synthetic environmental axes



TABLE 1. SPECIES PRESENCE (P = percent plots with species) AND MODAL COVER-ABUNDANCE VALUE (C)<sup>a</sup> FOR SPECIES WITH P > 20% IN AT LEAST ONE HABITAT TYPE. <sup>a</sup>1 = one specimen, 2 = sparse, 3 = less than 5%, 4 = 5–25%, 5 = 25–50%, 6 = 50–75%, 7 = 75–100%. <sup>b</sup>*Arnica longifolia*, *Lupinus polyphyllus*, and *Mimulus guttatus* restricted to type, but of low presence. <sup>c</sup>*Anemone drummondii* restricted to type, but of low presence. <sup>d</sup>The largest P + C for tree canopy, saplings and seedlings presented. See Riegel (1982) for complete differentiated table. <sup>e</sup>As reproduction only.

[illegible]



TABLE 1. CONTINUED.

|                                | (1)<br>POTR/<br>VECA <sup>b</sup><br>P/C | (2)<br>POTR/<br>ASFO<br>P/C | (3)<br>CELA/<br>BASA<br>P/C | (4)<br>ABCO/<br>LUCA<br>P/C | (5)<br>PIJE<br>phase<br>P/C | (6)<br>PIWA<br>phase<br>P/C | (7)<br>ABCO/<br>OSCH<br>P/C | (8)<br>ABCO/<br>PYPI<br>P/C | (9)<br>PIAL/<br>STCA<br>P/C | (10)<br>PIAL/<br>PEGR <sup>c</sup><br>P/C | (11)<br>PIAL/<br>ARAC<br>P/C |
|--------------------------------|--|-----------------------------|-----------------------------|-----------------------------|-----------------------------|-----------------------------|-----------------------------|-----------------------------|-----------------------------|---|------------------------------|
| <i>Deschampsia elongata</i>    | 22/2                                     |                             |                             |                             |                             |                             |                             |                             |                             |   |                              |
| <i>Delphinium nuttallianum</i> | 50/3                                     | 11/2                        |                             |                             |                             |                             |                             |                             |                             |   |                              |
| <i>Ranunculus occidentalis</i> | 44/2                                     | 5/2                         |                             |                             |                             |                             |                             |                             |                             |   |                              |
| <i>Festuca rubra</i>           | 25/4                                     | 22/3                        |                             |                             |                             |                             |                             |                             |                             |   |                              |
| <i>Nemophila breviflora</i>    | 33/2                                     | 45/3                        | 4/2                         |                             |                             |                             | 9/2                         |                             |                             |   |                              |
| <i>Arabis divaricarpa</i>      | 11/2                                     | 30/2                        | 4/2                         |                             |                             |                             |                             |                             |                             |   |                              |
| <i>Aster foliaceus</i>         | 11/3                                     | 85/4                        |                             |                             |                             |                             |                             |                             |                             |   |                              |
| <i>Eriogonum umbellatum</i>    |  |                             | 33/3                        |                             |                             |                             |                             |                             |                             |   |                              |
| <i>Balsamorhiza sagittata</i>  |  |                             | 58/4                        | 23/2                        | 35/2                        |                             |                             | 4/3                         |                             |   |                              |
| <i>Mertensia oblongifolia</i>  | 11/3                                     | 70/3                        | 4/2                         | 4/2                         | 3/3                         | 6/2                         |                             |                             |                             |   |                              |
| <i>Paeonia brownii</i>         |  | 25/3                        | 4/2                         | 12/3                        | 9/3                         | 17/3                        |                             |                             |                             |   |                              |
| <i>Lupinus argenteus</i>       |  | 20/5                        | 8/3                         | 13/3                        | 12/4                        | 17/2                        |                             |                             |                             |   |                              |
| <i>Eriophyllum lanatum</i>     |  | 5/3                         | 50/3                        | 17/3                        | 21/2                        | 11/2                        |                             |                             |                             |   |                              |
| <i>Eriogonum nudum</i>         |  |                             | 29/2                        | 10/3                        | 12/3                        | 6/2                         | 1/3                         |                             |                             | 6/3                                       |                              |
| <i>Erigeron inornatus</i>      |  |                             | 17/3                        | 22/3                        | 29/3                        | 6/3                         |                             |                             |                             |   |                              |
| <i>Phacelia humilis</i>        |  | 75/3                        | 4/2                         | 2/3                         |                             | 6/3                         | 7/2                         |                             |                             |   |                              |
| <i>Nemophila parviflora</i>    | 40/2                                     | 22/2                        | 8/2                         | 2/2                         |                             | 6/2                         | 4/2                         |                             |                             | 13/2                                      |                              |
| <i>Polygonum douglasii</i>     |  | 30/2                        |                             | 4/2                         |                             |                             | 7/2                         |                             |                             |   |                              |
| <i>Apocynum pumilum</i>        |  |                             | 4/2                         | 31/4                        | 6/2                         |                             |                             |                             |                             |   |                              |
| <i>Cryptantha torreyana</i>    |  | 35/2                        | 13/2                        | 6/2                         | 47/4                        | 28/2                        | 4/2                         | 3/2                         |                             |   |                              |
| <i>Elymus glaucus</i>          |  | 10/3                        | 29/3                        | 22/3                        | 9/2                         | 32/3                        | 4/2                         | 6/2                         |                             |   |                              |
| <i>Hydrophyllum capitatum</i>  | 56/2                                     | 60/3                        | 4/1                         | 12/2                        |                             | 33/2                        | 16/3                        | 3/1                         |                             |   |                              |
| <i>Chimaphila menziesii</i>    |  |                             |                             | 2/3                         |                             | 6/3                         | 29/3                        | 12/2                        |                             |   |                              |
| <i>Castilleja applegatei</i>   |  | 15/1                        | 46/3                        | 10/3                        |                             | 17/3                        | 3/2                         | 45/2                        |                             |   |                              |
| <i>Hieracium horridum</i>      |  | 5/3                         | 33/2                        | 40/3                        | 6/2                         | 28/2                        | 1/2                         | 6/2                         |                             |   |                              |
| <i>Silene menziesii</i>        |  |                             | 8/2                         | 25/3                        | 47/3                        | 39/2                        | 16/2                        | 33/3                        |                             |   |                              |
|                                |  |                             |                             |                             | 18/4                        |                             | 17/3                        | 12/3                        |                             |   |                              |



TABLE 1. CONTINUED.

|                               | (1)                               | (2)                  | (3)                  | (4)                  | (5)                  | (6)                  | (7)                  | (8)                  | (9)                  | (10)                              | (11)                 |
|-------------------------------|-----------------------------------|----------------------|----------------------|----------------------|----------------------|----------------------|----------------------|----------------------|----------------------|-----------------------------------|----------------------|
|                               | POTR/<br>VECA <sup>b</sup><br>P/C | POTR/<br>ASFO<br>P/C | CELA/<br>BASA<br>P/C | ABCO/<br>LUCA<br>P/C | PIJE<br>phase<br>P/C | PIWA<br>phase<br>P/C | ABCO/<br>OSCH<br>P/C | ABCO/<br>PYPI<br>P/C | PIAL/<br>STCA<br>P/C | PIAL/<br>PEGR <sup>c</sup><br>P/C | PIAL/<br>ARAC<br>P/C |
| <i>Smilacina racemosa</i>     |                                   |                      | 8/1                  | 25/1                 | 29/2                 | 17/1                 | 41/3                 | 24/2                 |                      |                                   |                      |
| <i>Phacelia hastata</i>       |                                   |                      | 13/2                 | 8/3                  | 3/2                  | 17/3                 | 33/2                 | 9/2                  |                      |                                   |                      |
| <i>Solidago canadensis</i>    |                                   |                      |                      | 35/4                 | 44/4                 | 17/2                 | 4/2                  | 3/2                  |                      |                                   |                      |
| <i>Pterospora andromedea</i>  |                                   |                      |                      | 23/2                 | 29/2                 | 11/3                 | 6/2                  | 42/2                 |                      |                                   |                      |
| <i>Calystegia polymorphus</i> |                                   |                      |                      | 22/3                 | 24/3                 | 17/4                 | 1/2                  | 3/2                  |                      |                                   |                      |
| <i>Hieracium albiflorum</i>   |                                   |                      |                      | 15/3                 | 12/3                 | 12/3                 | 39/3                 | 48/3                 |                      |                                   |                      |
| <i>Potentilla glandulosa</i>  | 11/3                              |                      |                      | 22/2                 | 24/2                 | 17/2                 | 14/2                 | 6/2                  | 17/2                 |                                   |                      |
| <i>Phlox diffusa</i>          |                                   |                      | 58/3                 | 8/2                  | 3/3                  | 17/2                 | 3/1                  | 3/2                  | 22/3                 | 6/2                               |                      |
| <i>Collomia linearis</i>      | 78/3                              | 45/3                 | 4/2                  | 27/2                 | 38/2                 | 6/2                  | 7/3                  | 9/2                  |                      |                                   |                      |
| <i>Senecio aronicoides</i>    | 11/2                              | 60/3                 | 33/3                 | 19/2                 | 15/2                 | 28/2                 | 13/3                 | 3/2                  |                      |                                   |                      |
| <i>Osmorhiza occidentalis</i> | 35/2                              | 56/2                 |                      | 4/2                  | 6/2                  |                      | 1/2                  |                      |                      | 6/2                               |                      |
| <i>Vicia americana</i>        | 56/3                              | 65/4                 |                      | 54/3                 | 56/3                 | 50/3                 | 39/3                 | 18/3                 | 4/4                  |                                   |                      |
| <i>Thalictrum fendleri</i>    | 44/2                              | 45/1                 |                      | 6/2                  | 3/2                  | 11/2                 | 39/2                 | 13/2                 |                      | 19/1                              |                      |
| <i>Achillea lanulosa</i>      | 67/3                              | 25/3                 | 4/2                  | 42/3                 | 44/3                 | 39/3                 |                      | 12/3                 | 4/3                  | 6/2                               |                      |
| <i>Collinsia parviflora</i>   | 33/3                              | 65/3                 |                      | 12/3                 | 12/3                 | 11/2                 | 26/3                 | 6/2                  | 17/3                 | 6/4                               |                      |
| <i>Osmorhiza chilensis</i>    |                                   |                      | 13/2                 | 48/3                 | 50/3                 | 44/3                 | 71/3                 | 69/3                 | 4/3                  | 25/2                              |                      |
| <i>Bromus marginatus</i>      | 44/3                              | 60/4                 | 17/2                 | 29/2                 | 26/2                 | 33/3                 | 20/2                 | 24/3                 |                      | 13/2                              | 7/2                  |
| <i>Agoseris glauca</i>        | 56/2                              | 30/3                 |                      | 19/2                 | 15/2                 | 22/2                 | 1/2                  |                      | 52/3                 | 25/3                              | 14/3                 |
| <i>Viola purpurea</i>         | 22/2                              | 65/3                 | 29/2                 | 17/2                 | 15/2                 | 22/2                 | 61/3                 | 9/2                  | 13/2                 | 50/3                              | 7/2                  |
| <i>Arenaria jamesiana</i>     | 22/3                              | 15/3                 | 13/2                 | 38/3                 | 38/3                 | 39/3                 | 51/5                 | 76/3                 | 4/3                  | 19/4                              |                      |
| <i>Arnica cordifolia</i>      | 5/4                               | 5/4                  | 17/2                 | 52/3                 | 15/2                 | 11/3                 | 25/4                 | 73/3                 | 4/2                  | 38/4                              | 14/2                 |
| <i>Poa nervosa</i>            | 5/2                               | 15/3                 | 25/2                 | 10/3                 | 3/3                  | 22/3                 | 12/3                 | 42/2                 | 65/3                 | 63/3                              | 29/3                 |
| <i>Stipa californica</i>      |                                   | 10/3                 | 21/3                 | 19/3                 | 21/3                 | 17/3                 | 16/3                 | 6/3                  | 87/5                 | 31/3                              | 21/3                 |
| <i>Stipa occidentalis</i>     |                                   | 5/3                  | 25/3                 | 23/3                 | 21/3                 | 28/3                 | 22/3                 | 6/3                  | 35/3                 | 25/3                              | 29/4                 |
| <i>Lupinus caudatus</i>       |                                   | 20/5                 | 8/2                  | 71/3                 | 79/3                 | 56/3                 | 23/3                 | 9/3                  |                      | 50/2                              | 29/3                 |
| <i>Penstemon gracilentus</i>  |                                   |                      | 8/2                  | 4/2                  |                      | 11/2                 | 36/3                 | 33/2                 | 30/3                 | 75/2                              | 21/2                 |







defined by linear combinations of the supplied environmental variables, including elevation, aspect, slope, and percent surface rock cover and topographic position (Gauch 1982).

Floristic relationships of the habitat types and phases are based on relative constancy and modal cover-abundance class of the definitive species found within a type or phase.

## RESULTS AND DISCUSSION

Four series, containing nine habitat types are recognized: *Cercocarpus ledifolius* (CELE), *Populus tremuloides* (POTR), *Abies concolor* (ABCO), and *Pinus albicaulis* (PIAL). One habitat type was further subdivided into phases.

Environmental data are presented by habitat type in Table 2. Means and ranges of height and cover for canopy, sapling, seedling, shrub, and herbaceous layers are presented in Table 3. Mean DBH and basal area are presented in Table 4.

*Cercocarpus ledifolius* (CELE) series. *Cercocarpus* is the dominant tree in a moderate canopy cover ( $\bar{x}$  = 35%) with a moderate shrub ( $\bar{x}$  = 25%) and moderate herbaceous cover ( $\bar{x}$  = 35%). Basal area is typically low with small stem (2.5–12.2 cm) diameters. This series is found on exposed xeric upper slopes and ridges. Surface rock cover is variable, but is the highest in the study area. Soils are typically very rocky, shallow, and poorly developed. Litter depth is the lowest of all the series.

The *Cercocarpus ledifolius*/*Balsamorhiza sagittata* (CELE/BASA) habitat type typically occurs on southeast aspects and occupies the steepest slopes inhabited by forests. Sapling cover is primarily composed of *Cercocarpus* and secondarily of *Juniperus occidentalis*. *Cercocarpus* is the sole species in the seedling layer. *Symphoricarpos vaccinioides* and *Artemisia tridentata* dominate the shrub layer; *Balsamorhiza sagittata* dominates the herbaceous layer. Conspicuous herbs include *Phlox diffusa*, *Eriophyllum lanatum*, *Castilleja applegatei*, *Senecio aronicoides*, *Eriogonum umbellatum*, and *E. nudum*.

*Vegetation dynamics.* *Cercocarpus ledifolius*, a characteristic Great Basin xerophyte (Gleason and Cronquist 1964), is typically found growing on rocky, and immature soils. Oosting (1956) considered *C. ledifolius* to be a component within a climax community. According to Dealy (1975) this small tree (sometimes taking a shrub form) expands its populations from relict seed trees that are protected from fire on rocky sites. However, the oldest trees (1350 years) occur in the Shoshone Range of central Nevada between 2591–3049 m, in deep well developed soils on north to northeast aspects, below ridgelines, where snow accumulation provides soil moisture late into the growing season (Schultz 1987; Schultz et al. 1990). Typically the



best developed stands are found on rocky sites protected from reoccurring fires as *C. ledifolius* is a weak sprouter (Wright et al. 1979). These sites may act as long-term refugia (Vasek and Thorne 1977).

Occasionally the CELE/BASA habitat type occurs on a small rocky island or rock bald with little or no soil, surrounded by entirely different vegetation. This type also can be found in areas of shallow soils within other forest types.

*Populus tremuloides* (POTR) series. *Populus* dominates the canopy and reproduction strata with moderate sized (7.7–42.7 cm) stems. Herbs dominate the vegetation under a variable tree canopy. Canopy cover ranges from open to dense (15–75%) with low shrub cover ( $\bar{x}$  = 7%) and high herb cover ( $\bar{x}$  = 76%). This series is commonly found on lower slopes with mesic to xeric conditions, on a broad variety of soils. Litter is relatively shallow.

The *Populus tremuloides*/*Veratrum californicum* (POTR/VECA) habitat type occurs on gentle slopes usually associated with seeps and streams with a western aspect. This type occurs in the most mesic areas of the study site. Soils are typically fine-textured, deep, and well developed. Surface soil moisture is evident throughout the growing season. Mean canopy cover of *Populus* is 33%. Sapling and seedling cover are moderate. *Symphoricarpos vaccinioides* and *Artemisia tridentata* are the only shrubs in this type, having a total mean cover of 1%. Herbaceous layer cover ( $\bar{x}$  = 79%) is the highest of all types. *Veratrum californicum* dominates the understory. Other typical herbs include *Delphinium nuttallianum*, *Ranunculus occidentalis*, *Festuca rubra*, and *Heracleum lanatum*.

The *Populus tremuloides*/*Aster foliaceus* (POTR/ASFO) habitat type occurs on gentle southeast facing slopes. Soils are typically coarse textured, moderately deep, and well developed. Mean canopy cover of *Populus* is 37%. *Symphoricarpos vaccinioides* and *Artemisia tridentata* dominate the patchy shrub layer with a total mean cover of 13%. Cover of the herbaceous layer is high ( $\bar{x}$  = 72%), and is dominated by *Aster foliaceus*. On less disturbed and mesic sites *Mertensia oblongifolia* is common.

*Vegetation dynamics.* The biology of *Populus tremuloides* has been extensively examined (DeByle and Winokur 1985). Since *P. tremuloides* is a fast-growing and generally short-lived tree, most view it as seral when it is found in association with shade-tolerant conifers or long-lived hardwoods. However, when pure *P. tremuloides* stands are found without associate conifers, it is assumed to replace itself (Mueggler 1988). Such stands are all-aged and most likely developed from root suckering (Jones and DeByle 1985). Recently, DeByle et al. (1987) estimated that fire frequencies of 100 to 300 years are necessary to regenerate and maintain *P. tremuloides*.

Stands of POTR/VECA and POTR/ASFO were selected because







TABLE 2. CONTINUED.

|  | Elevation<br>(m)  |         | Topography  |                            | Slope<br>(°) |         | Aspect             |         | Surface<br>rock cover<br>% |         | Depth of<br>forest<br>floor<br>(cm) |         |
|--|-------------------|---------|-------------|----------------------------|--------------|---------|--------------------|---------|----------------------------|---------|-------------------------------------|---------|
|  | mean              | min-max | mode        | min-max                    | mean         | min-max | mode               | min-max | mean                       | min-max | mean                                | min-max |
| <i>Abies concolor/Osmorhiza chilensis</i> type     | 2177<br>1878-2390 |         | mid slope   | near creek-ridge           | 17<br>2-40   |         | West<br>NNE-N      |         | 8<br>0-60                  |         | 6.1<br>1.2-14.0                     |         |
| <i>Abies concolor/Pyrola picta</i> type            | 2182<br>1829-2317 |         | upper slope | near creek-<br>upper slope | 20<br>6-40   |         | NNW<br>ENE-N       |         | 1<br>0-9                   |         | 4.1<br>0.3-14.0                     |         |
| <i>Pinus albicaulis/Stipa californica</i> type     | 2525<br>2253-2720 |         | upper slope | near creek-<br>upper slope | 14<br>3-26   |         | West<br>East-North |         | 6<br>0-45                  |         | 1.8<br>0-7.6                        |         |
| <i>Pinus albicaulis/Penstemon gracileutus</i> type | 2472<br>2329-2683 |         | upper slope | mid-slope-ridge            | 22<br>5-47   |         | NNE<br>NNE-North   |         | 8<br>0-40                  |         | 2.8<br>0-7.6                        |         |
| <i>Pinus albicaulis/Arenaria aculeata</i> type     | 2665<br>2427-2979 |         | ridge       | upper slope-<br>summit     | 22<br>2-36   |         | NW<br>NNE-WSW      |         | 20<br>0-80                 |         | 1.6<br>0-4.6                        |         |



TABLE 3. CANOPY, SAPLING, SEEDLING, SHRUB, AND HERB COVER AND HEIGHT BY FOREST HABITAT TYPE AND PHASE.

|   | Canopy cover % |                  | Height (m) |                  | Sapling cover % |            | Height (m)     |             | Seedling cover % |         | Shrub cover % |         | Height (m) |         | Herb cover % |         |
|---|----------------|------------------|------------|------------------|-----------------|------------|----------------|-------------|------------------|---------|---------------|---------|------------|---------|--------------|---------|
|   | mean           | min-max          | mean       | min-max          | mean            | min-max    | mean           | min-max     | mean             | min-max | mean          | min-max | mean       | min-max | mean         | min-max |
| <i>Cercocarpus ledifolius/Balsamorhiza sagittata</i> type | 35<br>10-60    | 3.4<br>2.4-4.8   | 1<br>1-5   | 0-0.6<br>0.3-2.4 | 0.3<br>1-1      | 25<br>1-65 | 0.6<br>0.3-1.5 | 35<br>15-70 |                  |         |               |         |            |         |              |         |
| <i>Populus tremuloides/Veratrum californicum</i> type     | 33<br>15-65    | 10.7<br>5.5-18.3 | 8<br>0-75  | 0.9<br>0-2.7     | 3<br>0-7        | 1<br>0-5   | 0.6<br>0.3-0.6 | 79<br>13-97 |                  |         |               |         |            |         |              |         |
| <i>Populus tremuloides/Aster foliaceus</i> type           | 37<br>15-75    | 9.1<br>4.6-18.3  | 9<br>0-60  | 1.5<br>0-3.7     | 2<br>0-10       | 13<br>0-45 | 0.6<br>0-0.9   | 72<br>30-90 |                  |         |               |         |            |         |              |         |
| <i>Abies concolor/Lupinus caudatus</i> type               | 44<br>10-75    | 19.8<br>6.1-36.6 | 12<br>0-35 | 2.1<br>0-5.5     | 3<br>0-18       | 15<br>1-65 | 0.8<br>0.2-2.1 | 58<br>6-90  |                  |         |               |         |            |         |              |         |
| <i>Pinus jeffreyi</i> phase                               | 46<br>10-70    | 20.1<br>6.1-33.5 | 12<br>3-35 | 2.1<br>0.9-3.7   | 2<br>0-7        | 11<br>1-40 | 0.8<br>0.3-2.1 | 60<br>6-88  |                  |         |               |         |            |         |              |         |
| <i>Pinus washoensis</i> phase                             | 42<br>25-75    | 18.9<br>6.1-33.5 | 13<br>0-30 | 2.1<br>0-4.0     | 4<br>0-18       | 22<br>2-65 | 0.8<br>0.3-1.8 | 54<br>35-90 |                  |         |               |         |            |         |              |         |
| <i>Abies concolor/Osmorhiza chilensis</i> type            | 62<br>20-90    | 18.6<br>4.6-36.6 | 14<br>1-45 | 2.4<br>1.2-4.9   | 3<br>0-15       | 5<br>0-15  | 0.6<br>0-0.9   | 37<br>5-80  |                  |         |               |         |            |         |              |         |



TABLE 3. CONTINUED.

|   | Canopy<br>cover %<br>mean<br>min-max | Height<br>(m)<br>mean<br>min-max | Sapling<br>cover %<br>mean<br>min-max | Height<br>(m)<br>mean<br>min-max | Seedling<br>cover %<br>mean<br>min-max | Shrub<br>cover %<br>mean<br>min-max | Height<br>(m)<br>mean<br>min-max | Herb<br>cover %<br>mean<br>min-max |
|---|--------------------------------------|----------------------------------|---------------------------------------|----------------------------------|--|-------------------------------------|----------------------------------|------------------------------------|
| <i>Abies concolor</i> / <i>Pyrola picta</i> type            | 56<br>15-90                          | 22.0<br>6.1-36.6                 | 28<br>2-90                            | 2.7<br>1.5-3.7                   | 4<br>1-10                              | 8<br>0-40                           | 0.6<br>0-0.9                     | 35<br>5-90                         |
| <i>Pinus albicaulis</i> / <i>Stipa californica</i> type     | 46<br>20-80                          | 11.3<br>6.1-18.3                 | 14<br>3-45                            | 2.7<br>0.9-3.7                   | 4<br>0-35                              | 1<br>0-15                           | 0.2<br>0-0.9                     | 58<br>20-85                        |
| <i>Pinus albicaulis</i> / <i>Penstemon gracilentus</i> type | 49<br>15-80                          | 9.1<br>3.4-18.3                  | 7<br>2-25                             | 1.8<br>0.6-3.0                   | 1<br>1-5                               | 10<br>0-50                          | 0.6<br>0-0.9                     | 32<br>15-70                        |
| <i>Pinus albicaulis</i> / <i>Arenaria aculeata</i> type     | 31<br>8-50                           | 6.4<br>3.0-13.7                  | 10<br>3-40                            | 1.8<br>0.6-3.7                   | 2<br>0-5                               | 1<br>0-8                            | 0.2<br>0-0.6                     | 49<br>3-80                         |



TABLE 4. BASAL AREA ( $\text{m}^2 \text{ ha}^{-1}$ ) AND STEM DBH (cm) BY SPECIES FOR *CERCOCARPUS LEDIFOLIUS*, *POPULUS TREMULOIDES*, *ABIES CONCOLOR* AND *PINUS ALBICAULIS* SERIES.

| Series/species   | Basal area mean/SD |             | DBH mean/SD range       |                         |
|--|--------------------|-------------|-------------------------|-------------------------|
|  | Live               | Dead        | Live                    | Dead                    |
| <i>Cercocarpus ledifolius</i><br>(n = 65 live) (n = 13 dead) | 33.67/7.01         | 7.65/7.01   | 7.12/2.33<br>2.5-12.2   | 4.33/1.79<br>2.0-8.3    |
| <i>Populus tremuloides</i><br>(n = 29 live) (n = 2 dead)     | 48.21/3.25         | 4.59/6.49   | 25.1/7.69<br>7.7-42.7   | 24.0/9.0<br>17.0-31.0   |
| <i>Abies concolor</i><br>(n = 32 live) (n = 2 dead)          | 74.61/14.21        | 6.89/2.65   | 21.61/15.09<br>5.5-75.0 | 16.35/10.12<br>9.2-23.5 |
| <i>Pinus albicaulis</i><br>(n = 31 live) (n = 9 dead)        | 33.67/10.60        | 18.37/12.15 | 23.59/14.29<br>4.9-57.3 | 30.41/15.21<br>8.2-60.8 |



they lack coniferous associates; however, some stands in the South Warner Mountains have *Abies concolor* and sometimes *Pinus* associates, particularly *P. contorta*. These stands are probably seral to ABCO series types. However, the suppression of fire and heavy grazing, characteristically associated with the POTR/ASFO, may favor the establishment of *A. concolor* and *P. contorta* (Mueggler 1985).

Heavy grazing probably has contributed to the abundance of *Veratrum californicum* in the POTR/VECA habitat type (Mueggler 1988). It is interesting to note that *Draba stenoloba* var. *ramosa* is almost exclusively found in the understory of *Veratrum*, suggesting a soil moisture and/or shade requirement. The abundance of *Aster foliaceus* and other forbs in the POTR/ASFO habitat type is also a probable response to cattle grazing (C. G. Johnson, Jr., pers. comm., Nov 1989).

*Abies concolor* (ABCO) series. *Abies* is the dominant species in the reproduction strata. Canopy cover varies from open to dense (10–90%) with low shrub ( $\bar{x}$  = 9%) and moderate herb cover ( $\bar{x}$  = 43%). Basal area is the highest of all series described, a function of many suppressed *Abies* growing beneath the canopy of large, older *Pinus* and *Abies* (5.5–75.0 cm). This series occupies more area and has the largest elevation range of all the series. It occurs from lower to upper slopes and is also found near creeks and on ridges. Soils are coarse textured, well drained, and moderately to highly developed. Litter is the deepest of all the series.

The *Abies concolor*/*Lupinus caudatus* (ABCO/LUCA) habitat type commonly occurs on lower west slopes but does range from creek side to ridges. Overstory is generally open but cover is quite variable (10–75%). *Pinus jeffreyi* dominates with lesser amounts of *Abies*. *Pinus washoensis* and *P. ponderosa* are associates with nearly equal constancy but with relatively low covers. *Abies* constitutes the majority of the regeneration in the sapling and seedling layers. Shrub cover is moderate ( $\bar{x}$  = 15%), often characterized by *Amelanchier pallida*. The herbaceous layer, dominated by *Lupinus caudatus*, has a moderately high cover ( $\bar{x}$  = 58%). Herbs definitive of this type include *Hieracium horridum*, *Solidago canadensis*, *Apocynum pumilum*, and *Silene menziesii*.

There are two phases within the ABCO/LUCA type: *Pinus jeffreyi* (PIJE) phase and *P. washoensis* (PIWA) phase. Though the shrub and herbaceous taxa are similar in the phases, their frequency and cover is greater in the *Pinus jeffreyi* phase.

The *Pinus jeffreyi* phase inhabits the lower to mid elevations 1670–2149 m on lower southwest slopes. Canopy cover averages 46%, with *Pinus jeffreyi* and *Abies* common. The sapling and seedling layers are mostly *Abies* and *Pinus jeffreyi*.



Conversely, the *Pinus washoensis* phase inhabits mid to upper elevations 1890–2195 m on north aspects. Mean canopy cover is 42% of mainly *Pinus washoensis* and *Abies*. *Abies* dominates the sapling and seedling strata.

The *Abies concolor/Osmorhiza chilensis* (ABCO/OSCH) habitat type characteristically occurs on midslopes on west aspects but can be found from creek to ridges. Canopy cover varies but has the highest mean cover (62%) of all types described. *Abies* is the dominant canopy tree. *Pinus albicaulis* is a higher elevation associate, whereas *P. washoensis*, *P. jeffreyi*, and *P. ponderosa* occur at mid- to lower elevations. *Abies* dominates reproduction in the sapling and seedling layers. Shrub cover is low ( $\bar{x} = 5\%$ ) with *Symphoricarpos vaccinioides* comprising half of the shrub layer. A moderate herbaceous cover ( $\bar{x} = 37\%$ ) is dominated by *Osmorhiza chilensis*. Other taxa characteristic of this type are *Smilacina racemosa* and *Phacelia hastata*.

The *Abies concolor/Pyrola picta* (ABCO/PYPI) habitat type characteristically occurs on upper northwesterly facing slopes. Mean canopy cover is 56%. *Abies* is the canopy dominant, and *Pinus monticola* a codominant. Other associated trees include *P. washoensis*, *P. albicaulis*, *P. ponderosa*, and *P. contorta*. Sapling cover ( $\bar{x} = 28\%$ ) is by far the highest of all the types. Mean cover of the shrub and herb layers are 8% and 35%, respectively. *Ribes viscosissimum* dominates the sparse shrub layer, *Pyrola picta* the herb layer. Other common herbs are *Arenaria jamesiana*, *Arnica cordifolia*, *Osmorhiza chilensis*, and *Hieracium albiflorum*.

*Vegetation dynamics.* *Abies concolor* reproduction is reduced in areas where lightning-caused fires are fairly frequent (U.S.D.A. 1965; Vale 1977). With fire suppression, *A. concolor* increases with a concurrent decrease in *Pinus* reproduction which together can result in a gradual change in structure and composition in ABCO/LUCA and ABCO/PYPI.

Overgrazing in *Artemisia tridentata*-steppe communities was responsible for the invasion and establishment of *A. concolor* trees (Vale 1975, 1977). Such invasion may account for the unusually xeric *A. concolor* stands and extent of ABCO/OSCH.

*Lupinus caudatus*, a palatable plant but poisonous to cattle and horses, is abundant in ABCO/LUCA. Its abundance may be a response to previous overgrazing (Hopkins 1979).

*The Pinus complex of the ABCO/LUCA type.* The ABCO/LUCA type is characterized by the occurrence of three diploxylon pines: *Pinus jeffreyi*, *P. ponderosa*, and *P. washoensis* all well studied in the area (Haller 1961, 1965; Smith 1967, 1971, 1981; Critchfield and Allenbaugh 1969; Griffin and Critchfield 1972; Critchfield 1984). The genetic, taxonomic, and ecological relationships of the pines in



northeastern California are complicated because *P. jeffreyi* and “good” *P. washoensis* reach their northeastern range limits here (Critchfield 1984; J.R. Haller pers. comm., July 1978). Also, the geographical-morphological transition from the more typical race of Pacific *P. ponderosa* to the North Plateau races of northeastern California to British Columbia and Montana occurs in this general area (Critchfield, 1984; J. R. Haller pers. comm., July 1978).

In contrast to Haller’s (1961) observations, we found that *P. jeffreyi* has a greater elevation range within the Wilderness Area than *P. ponderosa* and *P. washoensis*. There are few pure stands, however, of *P. jeffreyi* within the area, which is probably because purer, lower elevation stands do not occur within the elevation range (1457 m) of the wilderness boundary. “Good” individual representatives of *P. jeffreyi* are rare and occur on exposed xeric sites at approximately 2238 m. The lower elevation *P. jeffreyi* presented no problem in identification, but, at mid-elevations (1921–2043 m), *P. ponderosa* appeared quite varied with many possible intermediates with *P. washoensis*. The majority of *P. washoensis* was found as a codominant, in the lower to mid elevation (1890–2195 m) ABCO/OSCH type. At higher elevations (2043–2195 m), *P. washoensis* was the dominant pine.

*Pinus albicaulis* (PIAL) series. *Pinus albicaulis* dominates or shares the dominance of the canopy, sapling and seedling layers with *P. contorta*. Canopy cover generally is moderately open ( $\bar{x}$  = 42%), with low shrub ( $\bar{x}$  = 4%) and moderate herb ( $\bar{x}$  = 46%) cover. Basal area is low with considerable variation in stem diameters (4.9–57.3 cm). This series is found from upper slopes to summits. Soils are typically coarse textured, excessively drained and poorly developed. Surface rock cover is highly variable. Litter depth is typically shallow.

The *Pinus albicaulis*/*Stipa californica* (PIAL/STCA) habitat type typically inhabits upper slopes on western aspects, but can also be found near streams or springs. Canopy cover is moderate ( $\bar{x}$  = 46%); however, *Pinus albicaulis* and *P. contorta* cover is highly variable. In the sapling layer both occur with equal constancies, but with a lower cover than in the canopy. *Symphoricarpos vaccinioides* dominates the sparse cover ( $\bar{x}$  = 1%) of the shrub layer. The herb layer has moderately high mean cover of 58% and is dominated by *Stipa californica*. Important herbs are *Calyptridium umbellatum*, *Poa nervosa*, *Agoseris glauca*, *Stipa occidentalis*, and *Phlox diffusa*.

The *Pinus albicaulis*/*Penstemon gracilentus* (PIAL/PEGR) habitat type commonly inhabits upper northeast facing slopes, but also occurs on high ridges. Canopy cover is moderate ( $\bar{x}$  = 49%). *Pinus albicaulis* is the dominant and *P. contorta* is an infrequent associate. Sapling and seedling cover is low with similar proportions. Shrub cover is sparse ( $\bar{x}$  = 1%) with *Ribes montigenum* the dominant. Herb



cover is moderate ( $\bar{x} = 32\%$ ) but highly variable. Taxa descriptive of this type are *Penstemon gracilentus*, *Poa nervosa*, *Frasera speciosa*, and *Anemone drummondii*.

The *Pinus albicaulis*/*Arenaria aculeata* (PIAL/ARAC) habitat type characteristically occurs on upper northwest facing slopes to the summits where some trees form krummholz. Canopy over ( $\bar{x} = 31\%$ ) is the sparsest within the study. *Pinus albicaulis* dominates both the canopy and sapling strata. *Pinus contorta* occurs as an infrequent associate at the lower elevations within this type. *Ribes montigenum* and *Haplopappus bloomeri* dominate the sparse cover ( $\bar{x} = 1\%$ ) shrub layer. *Arenaria aculeata* dominates a moderate cover ( $\bar{x} = 49\%$ ) herb layer. Important herbs are *Penstemon davidsonii*, *Arabis lyallii*, *Trisetum spicatum*, *Raillardella argentea*, *Castilleja arachnoidea*, and *Senecio fremontii*.

*Vegetation dynamics.* Within PIAL/STCA, *Pinus albicaulis* and *P. contorta* appear to reproduce with near equal frequencies. Despite Vale's (1977) prediction that *P. contorta* is decreasing and *P. albicaulis* is increasing because of lack of fire, our data suggest that both are successfully reproducing and are persistent. *Pinus albicaulis* is also more drought and cold tolerant than *P. contorta* (Parsons 1980; Arno and Hoff 1989).

Above 2713 m, *Pinus albicaulis* is the canopy and reproductive dominant whereas *P. contorta* is only occasional. Our observations of fire-scarred trees and pieces of charcoal on the soil surface suggest an increase of fire with increasing elevation. The structure of the higher elevation stands does not favor rapid spread of ground fires. Higher elevation lightning-caused fires usually self-extinguish for lack of fuel. Other reasons seem better to explain the decreasing numbers of *P. contorta* with increasing elevations. It may be that the wider ecological amplitude of *P. albicaulis* allows it to increase in dominance in subalpine environments (Rundel et al. 1977; Arno and Hammerly 1984; Arno and Hoff 1989).

An alpine zone has been indicated for the South Warner Mountains (Major and Taylor 1977). Tree limit of *Pinus albicaulis* does not exist on any summit, including Eagle Peak, the highest in the Warner Mountains. Both flagged krummholz and cushion krummholz (Arno and Hammerly 1984) trees occur on very exposed and rocky sites, usually in the protection of large rocks, but, more commonly, stunted trees 1.8–3 m in height occur near the summits.

The summits along the crest of the South Warner Mountains provide habitat for many species known from the alpine zone in California (Munz 1973; Major and Taylor 1977), including *Arabis lemonii*, *A. lyallii*, *Calyptridium umbellatum*, *Oxyria digyna*, *Castilleja arachnoidea*, *Penstemon davidsonii*, *Ivesia gordonii*, *Lupinus lyallii*, *Senecio fremontii*, and *Raillardella argentea*. Few of these



species are restricted to alpine environments, but instead are typical of subalpine and even open montane habitats. Hence, both forest structure and species composition of the summit area of Eagle Peak indicate a subalpine, not alpine, vegetation.

*Vegetation pattern and the environment.* Inferred environmental variables were analyzed with direct gradient and principal component analyses (Fig. 1). Habitat types occur along elevation and soil moisture gradients. POTR/VECA is proximate to seeps, springs, and streams. POTR/ASFO occurs from moderately mesic to superficially xeric sites. Both types appear to be associated with sub-irrigated soils at a wide range of elevations. CELE/BASA is associated with dry and poorly developed soils. ABCO and PIAL habitat types are found along a well-defined elevation, soil moisture gradient. Hence, CELE and POTR are primarily edaphically controlled, whereas the coniferous forest types are more influenced by environmental variables that change with elevation.

The orographic effect also affects the patterning of vegetation. Forests on the gentle west slope are more extensive than those of the steeper, rockier east slope. However, floristic composition and environmental variables were found to be equivalent for the purpose of classification.

*Relationship to other vegetation types.* The forest vegetation in the South Warner Mountains is most similar floristically and ecologically to the North Warner Mountains in Oregon. Hopkins (1979) described two plant associations that are restricted to the North Warner Mountains in Oregon. His white fir-ponderosa pine-western white pine/sticky currant (*Ribes viscosissimum*) association is similar to our ABCO/PYPI habitat type. Both are found strictly on northerly aspects on mid- to upper slopes within similar elevation ranges. Hopkins's (1979) lodgepole pine-whitebark pine-western white pine/sandwort (*Arenaria kingii*) association resembles our PIAL/STCA habitat type except for the absence of *Abies concolor*, *Pinus monticola*, and *Arctostaphylos nevadensis*. Other vegetation classifications in central and southeastern Oregon have described forest types that are similar to our habitat types (Franklin and Dyrness 1973; Hopkins 1979; Volland 1976). Though overstory conifer composition may be different, understory vegetation is strikingly similar.

Smith et al. (1988) described four forest ecological types that occur in the Warner Mountains of California. Two are restricted by soil type and landform north of Cedar Pass. On Buck Mountain, the *Pinus washoensis*/*Arctostaphylos nevadensis*/*Poa nervosa* type occurs on soils derived from rhyolite and obsidian and is comprised solely of *P. washoensis*. Near Lassen Creek, the *Pinus ponderosa*/*Amelanchier pallida*-*Ceanothus velutinus*/*Arnica cordifolia* type is found only on scarps and is solely comprised of *P. ponderosa*. South



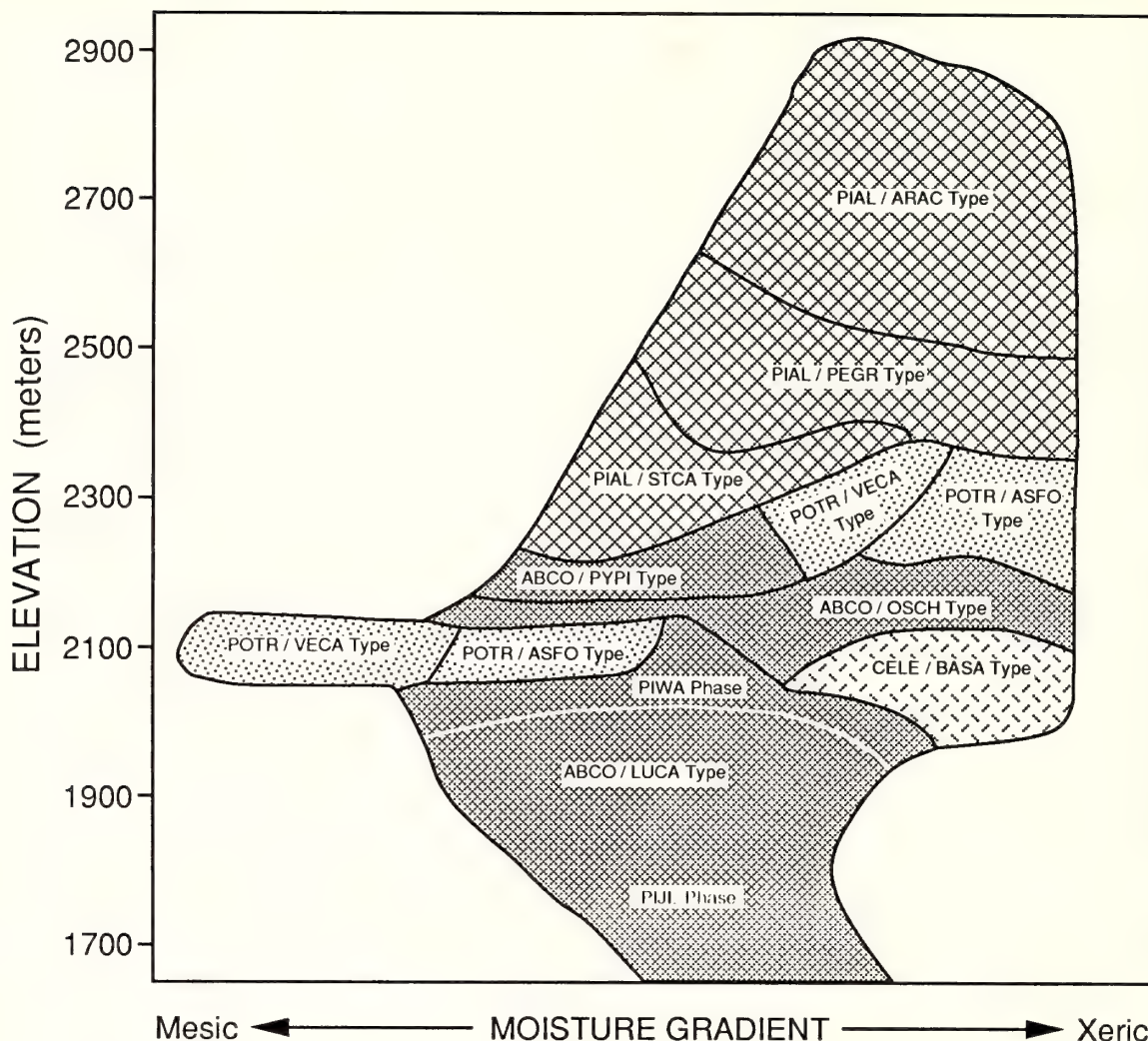


FIG. 1 Approximate distribution of South Warner Mountains forest habitat types along soil moisture and elevation gradients incorporating a principal component analysis and direct gradient analysis. Abbreviations equal the following type and phase names: *Cercocarpus ledifolius/Balsamorhiza sagittata* (CELE/BASA) type, *Populus tremuloides/Veratrum californicum* (POTR/VECA) type, *Populus tremuloides/Aster foliaceus* (POTR/ASFO) type, *Abies concolor/Lupinus caudatus* (ABCO/LUCA) type, *Pinus jeffreyi* (PIJE) phase, *Pinus washoensis* (PIWA) phase, *Abies concolor/Osmorhiza chilensis* (ABCO/OSCH) type, *Abies concolor/Pyrola picta* (ABCO/PYPI) type, *Pinus albicaulis/Stipa californica* (PIAL/STCA) type, *Pinus albicaulis/Pentstemon gracilentus* (PIAL/PEGR) type, and *Pinus albicaulis/Arenaria aculeata* (PIAL/ARAC) type. The empty area represents types that do not exist or are unsampled.

of Cedar Pass, the *Pinus washoensis/Symphoricarpos vaccinioides/Bromus orcuttianus* type is found on soil derived from basalt. Our PIWA phase of the ABCO/LUCA habitat type is an extension in geographical area of the latter type. The fourth type, *Pinus ponderosa-Abies concolor/Amelanchier pallida/Poa nervosa*, is found scattered throughout the west side of the northern Warner Mountains and appears very similar to our ABCO/LUCA habitat type. *Pinus jeffreyi* and *P. washoensis* are absent from their type whereas *Arc-tostaphylos nevadensis* is absent from ours.



The PIJE phase within the ABCO/LUCA habitat type is similar to vegetation described by Vasek (1978) in *Pinus jeffreyi* stands in southwestern Modoc Co. Differences include lower cover of *A. concolor* in Vasek's sites and the absence of *Calocedrus decurrens* in the southern Warner Mountains.

In the Whitehorse Mountains, near the Nevada border of southeastern Oregon, Dealy (1975) described a *Balsamorhiza sagittata* phase within a *Cercocarpus ledifolius*/*Symphoricarpos oreophilus* community that has both environmental and floristic similarities to our CELE/BASA habitat type. POTR/VECA communities have been described on deep, moist, poorly drained soils in the Uinta Mountains, Wasatch Range, and San Pitch Mountains of Utah (Mueggler 1988), in the Santa Rosa, Independence, and Jarbridge ranges in northern Nevada (Mueggler 1988), and in northwestern Colorado (Hoffman and Alexander 1980).

#### ACKNOWLEDGMENTS

We thank S. Bicknell, B. G. Smith, D. Keil, V. Holland, T. Keeler-Wolf, J. Shevock, for improving this manuscript. Jack Major stimulated our interest in the Warner Mountains. J. R. Haller verified specimens of *Pinus washoensis* and provided unpublished interpretation of this taxon. C. G. Johnson, Jr., U.S.F.S Region 6 Area Ecologist, provided insight on grazing and plant response. D. Goforth, T. Nelson, T. Prendusi, and J. Whipple of the Humboldt State Univ. Herbarium aided in plant identification. D. Bailey, J. Stumbos, S. and B. Bales, G. Schoolcraft, and R. Hanson made our field work enjoyable. We are grateful to personnel of the Modoc National Forest, especially Sidney Smith, for their interest and helpful suggestions. This study was supported in part by McIntire-Stennis Cooperative Forestry Research Project 57.

#### LITERATURE CITED

- ARNO, S. F. and R. P. HAMMERLY. 1984. Timberline: mountain and arctic forest frontiers. The Mountaineers, Seattle, WA.
- and R. J. HOFF. 1989. Silvics of whitebark pine (*Pinus albicaulis*). U.S.D.A. For. Serv. Gen. Tech. Rep. INT-253.
- CRITCHFIELD, W. B. 1984. Crossability and relationships of Washoe pine. *Madroño* 31:144–170.
- and G. L. ALLENBAUGH. 1969. The distribution of Pinaceae in and near northern Nevada. *Madroño* 19:12–26.
- CRONQUIST, A., A. H. HOLMGREN, N. H. HOLMGREN, and J. L. REVEAL. 1972. Intermountain flora, vascular plants of the Intermountain West, USA, Vol. 1. Hafner Publ. Co., New York.
- DAUBENMIRE, R. F. 1968. Plant communities: a textbook of plant synecology. Harper and Row, New York.
- DEALY, J. E. 1975. Ecology of curleaf mountain-mahogany (*Cercocarpus ledifolius* Nutt.) in eastern Oregon and adjacent areas. Ph.D. thesis. Oregon State Univ., Corvallis.
- DEBYLE, N. V. and R. P. WINOKUR. 1985. Aspen: ecology and management in the western United States. U.S.D.A. For. Serv. Gen. Tech. Rep. RM-119.
- , C. D. BEVINS, and W. C. FISCHER. 1987. Wildfire occurrence in aspen in the interior western United States. *W. J. Appl. For.* 2:73–76.



- DUFFIELD, W. A. and R. D. WELDIN. 1976. Mineral resources of the South Warner Wilderness, Modoc County, California. California Geol. Surv. Bull. 1385-D. U.S. Gov. Printing Office, Washington, D.C.
- FRANKLIN, J. F. and C. T. DYRNESS. 1973. Natural vegetation of Oregon and Washington. U.S.D.A. For. Serv. Gen. Tech. Rep. PNW-8.
- GAUCH, H. G., JR. 1982. Multivariate analysis in community ecology. Cambridge Univ. Press, Cambridge.
- GLEASON, H. A. and A. CRONQUIST. 1964. The natural geography of plants. Columbia Univ. Press, New York.
- GRIFFIN, J. R. and W. B. CRITCHFIELD. 1972. The distribution of forest trees in California. U.S.D.A. For. Serv. Res. Pap. PSW-82.
- HALLER, J. R. 1961. Some recent observations on ponderosa, Jeffrey, and Washoe pine in northeastern California. *Madroño* 16:126-132.
- . 1965. *Pinus washoensis* in Oregon: taxonomic and evolutionary implications. *Amer. J. Bot.* 52:646.
- HARPER, K. T., D. C. FREEMAN, W. K. OSTLER, and L. C. KILKOFF. 1978. The flora of the Great Basin mountain ranges: diversity, sources, and dispersal ecology. *Great Basin Naturalist Mem.* 2:81-103.
- HOFFMAN, G. R. and R. R. ALEXANDER. 1980. Forest vegetation of the Routt National Forest in northwestern Colorado: a habitat type classification. U.S.D.A. For. Serv. Res. Pap. RM-221.
- HOPKINS, W. E. 1979. Plant associations of the Fremont National Forest. U.S.D.A. For. Serv. Pac. Northwest Region R6-ECOL-79-004.
- JONES, J. R. and N. V. DEBYLE. 1985. Morphology. Pp. 11-24 in N. V. DeByle and R. P. Winokur (eds.), *Aspen: ecology and management in the western United States*. U.S.D.A. For. Serv. Gen. Tech. Rep. RM-119.
- LUCKOW, K. 1986. Soil survey of Modoc National Forest area, California. U.S.D.A. For. Serv. and Soil Conserv. Serv. in cooperation with the Univ. of Calif. Unpublished manuscript of file at U.S.D.A. For. Serv. Modoc National Forest, Alturas, CA.
- MACDONALD, G. A. and T. E. GAY, JR. 1966. Geology of the southern Cascade range, Modoc Plateau and the Great Basin areas in northeastern California. Pp. 43-48 in *Mineral resources report part I*. Calif. Div. of Mines and Geol. Sacramento, CA.
- MAJOR, J., and D. W. TAYLOR. 1977. Alpine. Pp. 601-675 in M. G. Barbour and J. Major (eds.), *Terrestrial vegetation of California*. Wiley Interscience, New York.
- MUEGGLER, W. F. 1985. Vegetation associations. Pp. 45-55 in N. V. DeByle and R. P. Winokur (eds.), *Aspen: ecology and management in the western United States*. U.S.D.A. For. Serv. Gen. Tech. Rep. RM-119.
- . 1988. Aspen community types of the intermountain region. U.S.D.A. For. Serv. Gen. Tech. Rep. INT-250.
- MUELLER-DOMBOIS, D. and H. ELLENBERG. 1974. *Aims and methods of vegetation ecology*. John Wiley and Sons Inc., New York.
- MUNZ, P. A. 1973. *A California flora and supplement*. Univ. of Calif. Press, Berkeley.
- ORLOCI, L. 1967. An agglomerative method for classification of plant communities. *J. Ecol.* 55:193-206.
- OOSTING, H. J. 1956. *The study of plant communities*. 2nd ed. W. H. Freeman and Co., San Francisco.
- PARSONS, D. J. 1980. California mixed subalpine. Pp. 90-91 in F. H. Eyre (ed.), *Forest cover types of the United States and Canada*. Soc. of Amer. For., Washington, D.C.
- PEASE, R. W. 1965. Modoc County: a geographic time continuum on the California volcanic tableland. *Univ. Calif. Publ. Geogr.* 17:1-304.



- PFISTER, R. D., B. L. KOVALCHIK, S. F. ARNO, and R. C. PRESBY. 1977. Forest habitat types of Montana. U.S.D.A. For. Serv. Gen. Tech. Rep. INT-34.
- PFISTER, R. D. and S. F. ARNO. 1980. Classifying forest vegetation habitat types based on potential climax vegetation. *For. Sci.* 26:52-70.
- RAVEN, P. H. 1977. The California flora. Pp. 601-675 in M. G. Barbour and J. Major (eds.), *Terrestrial vegetation of California*. Wiley Interscience, New York.
- RAVEN, P. H. and D. I. AXELROD. 1978. Origin and relationships of the California flora. *Univ. Calif. Publ. Bot.* 72:1-134.
- REVEAL, J. L. 1979. Biogeography of the Intermountain region. *Mentzelia*, J. N. Nevada Native Pl. Soc. 4:1-92.
- RIEGEL, G. M. 1982. Forest habitat types of the South Warner Mountains, Modoc County, northeastern California. M.S. thesis. Humboldt State Univ., Arcata, CA.
- and G. D. SCHOOLCRAFT. 1990. A checklist of the vascular plants of the South Warner Mountains, California. Humboldt State Univ. Herb. Spec. Publ. No. 3, Arcata, CA.
- RUNDEL, P. W., D. J. PARSONS, and D. T. GORDON. 1977. Montane and subalpine vegetation of the Sierra Nevada and Cascade Ranges. Pp. 559-599 in M. G. Barbour and J. Major (eds.), *Terrestrial vegetation of California*. Wiley Interscience, New York.
- SAWYER, J. O. 1975. Site moisture equivalency index. Unpublished manuscript on file at Humboldt State Univ., Arcata, CA.
- SCHULTZ, B. W. 1987. Ecology of curleaf mountain mahogany (*Cercocarpus ledifolius*) in western and central Nevada: population and structure dynamics. M.S. thesis. Univ. Nevada, Reno.
- SCHULTZ, B. W., P. T. TUELLER, and R. J. TAUSCH. 1990. Ecology of curleaf mahogany in western and central Nevada: community and population structure. *J. Range Manage.* 43:13-20.
- SMITH, R. H. 1967. Monoterpene composition of the wood resin of Jeffrey, Washoe, and Coulter, and lodgepole pines. *For. Sci.* 13:246-252.
- . 1971. Xylem monoterpenes of *Pinus ponderosa*, *P. washoensis* and *P. jeffreyi* in the Warner Mountains of California. *Madroño* 21:26-32.
- . 1981. Variation in immature cone color of ponderosa pine (Pinaceae) in northern California and southern Oregon. *Madroño* 28:272-275.
- SMITH, S., K. LUCKOW, and G. KLIEWER. 1988. Draft ecological types for the eastside pine ecosystem, Klamath, Modoc, Lassen, Plumas, Shasta-Trinity and Tahoe National Forests. U.S.D.A. For. Serv. Region 5. Unpublished manuscript on file at U.S.D.A. For. Serv. Modoc National Forest, Alturas, CA.
- STATE OF CALIFORNIA. 1980. California rainfall summary: monthly total precipitation, 1844-1979. Dept. of Water Resources, Sacramento, CA.
- . 1981. Snow survey measurements. Dept. of Water Resources Bull. 129-70, Sacramento, CA.
- U.S.D.A. 1965. Silvics of the forest trees of the United States. U.S.D.A. For. Serv. Ag. Handbook 271, Washington, D.C.
- U.S.D.C. WEATHER BUREAU. 1970. Observing Handbook No. 2, Sub Station Observations, Washington, D.C.
- VALE, T. R. 1975. Invasion of big sagebrush (*Artemisia tridentata*) by white fir (*Abies concolor*) on the southeastern slopes of the Warner Mountains, California. *Great Basin Naturalist* 35:319-324.
- . 1977. Forest changes in the Warner Mountains, California. *Ann. Assoc. Amer. Geogr.* 67:28-45.
- VASEK, F. C. 1978. Jeffrey pine and the vegetation of the southern Modoc National Forest. *Madroño* 25:9-30.
- , and R. F. THORNE. 1977. Transmontane coniferous vegetation. Pp. 797-832 in M. G. Barbour and J. Major (eds.), *Terrestrial vegetation of California*. Wiley Interscience, New York.



- VOLLAND, L. A. 1976. Plant communities of the central Oregon pumice zone. U.S.D.A. For. Serv. Pac. Northwest Region R6 Area Guide 2.
- WARD, J. H. 1963. Hierarchical grouping to optimize an objective function. J. Amer. Stat. Assoc. 58:236–244.
- WINKLER, D. W. and G. DANA. 1977. Summer birds of the lodgepole-aspen forest in the southern Warner Mountains, California. Western Birds 8:45–62.
- WRIGHT, H. A., L. F. NEUENSCHWANDER, and C. M. BRITTON. 1979. The role and use of fire in sagebrush-grass and pinyon-juniper plant communities. A state of the art review. U.S.D.A. For. Serv. Gen. Tech. Rep. INT-58.

(Received 28 Sep 1988; revision accepted 15 Dec 1989.)

---

## NOTEWORTHY COLLECTIONS

### CALIFORNIA

*MALOSMA LAURINA* (Nutt. in Torrey & A. Gray) Nutt. ex Abrams (ANACARDIACEAE).—San Luis Obispo Co., outskirts of Arroyo Grande, hills on W side of Oak Park Rd, ca. 0.5 km N from jctn with Noyes Rd, population of ca. 20 shrubs in *Quercus agrifolia* woodland, 16 Mar 1990, D. Keil 21343 with L. D. Oyler (OBI); large shrubs scattered in coastal scrub and chaparral on hills E of Hwy 227, N of Arroyo Grande, ca. 0.5 km S from jctn with Noyes Rd, 20 Mar 1990, D. Keil 21346 with V. L. Holland (OBI).

*Previous knowledge.* Coastal hills and mountains along Pacific slope from Santa Ynez Mts. of Santa Barbara Co., California to middle of Baja California peninsula (Munz, *A California Flora*, 1959; Smith, *Flora of the Santa Barbara region, California*, 1976; Wiggins, *Flora of Baja California*, 1980).

*Significance.* First records for San Luis Obispo Co., a northward range extension of ca. 70 km. *Rhus integrifolia* Nutt., similarly disjunct from Santa Barbara Co., was present in chaparral on the site where Keil 21346 was collected. Keil et al. (Madroño 32:214–224, 1985) reported *R. integrifolia* as new to San Luis Obispo County from a site ca. 0.5 km N of this location.

Smith (l.c.) noted that *M. laurina* is frequently planted along highways in Santa Barbara County. Human introduction of *M. laurina* into San Luis Obispo County cannot be ruled out; species exotic to the site (e.g., *Eucalyptus globulus* and *Pinus radiata*) are well-established in areas near the site for Keil 21346. In any case *M. laurina* is well established and reproducing in the Arroyo Grande area.—DAVID J. KEIL, Biological Sciences Department, California Polytechnic State University, San Luis Obispo, CA 93407.



## AN INVESTIGATION INTO THE STATUS OF *IRIS THOMPSONII* (IRIDACEAE)

CAROL A. WILSON,<sup>1</sup> ALFRED LEVINSON,<sup>2</sup> and RICHARD PETERSEN<sup>1</sup>

<sup>1</sup>Department of Biology, <sup>2</sup>Department of Chemistry,  
Portland State University, Portland, OR 97207

### ABSTRACT

Within *Iris* series *Californicae*, experimental hybrids between species are readily produced and natural hybrids have been reported as common. *Iris thompsonii* from the northwestern slopes of the Klamath Mountains has been described as a natural hybrid between *I. douglasiana* and *I. innominata*. The purpose of this study was to investigate the relationships of these three species and in particular to determine the status of *I. thompsonii*. Methods used were discriminant and cluster analyses of morphological characters and a chemotaxonomic analysis of flavonoid pigments using thin layer chromatography. The thirteen populations studied were found to represent three species: *I. douglasiana*, *I. innominata*, and *I. thompsonii*. This study does not support the current taxonomy for *I. thompsonii* that places this taxon within *I. innominata* as a color form or occasional hybrid between *I. innominata* and *I. douglasiana*.

The series *Californicae* (Diels) G. Lawr. in the genus *Iris* (Iridaceae) comprises approximately 16 closely related taxa that are thought to form a natural group. These taxa are distributed along the Pacific Coast in Washington, Oregon, and California. Numerous studies (e.g., Foster 1937; Lenz 1958; Clarkson 1959; Carter and Brehm 1969) have cited the occurrence of intraspecific variation and interspecific hybridization as sources of confusion in the systematics of the series.

The taxa under consideration in this study, *Iris douglasiana* Herbert, *I. innominata* L. Henderson, and *I. thompsonii* R. Foster, are found in the Klamath Mountains of southwestern Oregon and northern California. A major serpentine soil area occupies much of the study site. Serpentine areas are characterized by infertile, sparsely vegetated areas and species rich, endemic floras. Speciation in serpentine floras is thought to result from edaphic factors, specifically a combination of heavy metal toxicity and low nutrient levels (Kruckeberg 1954, 1986; Walker 1954). The three species occupy different habitats within this region. *Iris douglasiana* is typically found on grassy headlands along the coast, rarely more than two kilometers inland. *Iris innominata* inhabits inland rocky mountainous sites with sparse vegetation. *Iris thompsonii* is also an inland species but occurs on less sparse sites where a grass understory is generally present.

The series *Californicae* is often separated into three groups based



on perianth tube length. The intermediate perianth tube group consists of only these three species. *Iris douglasiana* is easily recognized by its large stature, wide leaves, and inflorescences with several flowers. Differences between *I. innominata* and *I. thompsonii* are less obvious and have led to some controversy. Both species are rather small with relatively narrow leaves and one (or sometimes two in *I. thompsonii*) flowers. Flower color in all three species has been reported to be variable. The most recent studies of the taxonomic relationships of the species did not lead to a consensus. Lenz (1958, 1959a) recognized *I. douglasiana* and *I. innominata* but retained *I. thompsonii* within *I. innominata*, considering some populations to be a hybrid between the two species and others to represent a color form of *I. innominata*. Clarkson (1962) retained *I. thompsonii* as a separate species although he considered it a probable hybrid between *I. douglasiana* and *I. innominata*. The purpose of this study was to investigate the status of these three species—within their area of sympatry.

Numerical analyses of selected characters and flavonoid studies were undertaken to: 1) determine what taxa are represented by the populations studied; 2) evaluate the relative amount of intra- and interspecific variation present; and 3) investigate the possible hybrid origin of *I. thompsonii*.

## METHODS

Thirteen populations (Table 1, Fig. 1) representing the range in which the three species can be found sympatrically were chosen as study sites. All of the study populations are located in southwestern Oregon except the Smith River population from adjacent Del Norte County, California. *Iris thompsonii* is known from just south of Powers in Coos County, Oregon, southward into northern Del Norte County, California. The range of *I. innominata* is entirely within Oregon in the northern portion of the study area from just west of Iron Mountain in Curry County, Oregon, eastward to Wolf Creek in Douglas County. *Iris douglasiana* is found along the coast from Coos Bay in Coos County south to Santa Barbara County, California. The three species are sympatric in the northern part of the study area to the west and to the south of Iron Mountain. *Iris thompsonii* and *I. douglasiana* are also sympatric in the southern portion of the study area along the Rogue and Smith rivers.

*Numerical Studies.* Floral and vegetative parts were collected from 10 to 25 individuals per population during the years of 1981, 1982, 1984, 1985, 1987, and 1988. Measurements taken were: stem length, number of cauline leaves, leaf width, number of flowers per inflorescence, bract length, bract width, petal length, petal width, sepal length, sepal width, stigma length, stigma width, stigma lobe length,



TABLE 1. COLLECTION SITE DATA FOR THIRTEEN POPULATIONS OF *IRIS* SPECIES FROM SOUTHWESTERN OREGON AND NORTHERN CALIFORNIA (Fig. 1). <sup>1</sup>Forest Service Rd 333 is the road between Agness and Powers. <sup>2</sup>Forest Service Rd 325 is the road between 333 and Humbug Mountain State Park.

| Population       | Collection data  |
|------------------|--|
| Daphne Grove     | OR: Coos Co., 2.4 mi S of Daphne Grove Campground on Rd 333 <sup>1</sup> .             |
| Iron Mountain I  | OR: Curry Co., 0.5 mi S of county line on Rd 333.                                      |
| Road 333         | OR: Curry Co., 5.1 mi S of county line on Rd 333.                                      |
| Road 3400        | OR: Curry Co., 450 yd. E along rd on N bank of Shasta Coast Cr.                        |
| Road 3406        | OR: Curry Co., 0.8 mi E along rd on N bank of South Cr.                                |
| Cape Blanco      | OR: Curry Co., Cape Blanco Park.   |
| Iron Mountain II | OR: Curry Co., 11 mi W of junction with Rd 333 on Rd 325 <sup>2</sup> .                |
| Champion Park    | OR: Curry Co., roadbank at Champion Park.  |
| Meyers Creek     | OR: Curry Co., where Meyers Cr. crosses U.S. 101.                                      |
| Carpenterville   | OR: Curry Co., 8.1 mi N of U.S. 101 on Carpenterville loop.                            |
| Snaketooth       | OR: Curry Co., 19.5 mi E of U.S. 101 along rd following the main fork of the Chetco R. |
| Chetco River     | OR: Curry Co., 4 mi E of U.S. 101 along rd on N bank of Chetco R.                      |
| Smith River      | CA: Del Norte Co., Jedediah Smith State Park.  |

peduncle length, and perianth tube length. A qualitative evaluation of flower color also was recorded.

Cluster analysis was employed using a modification of Hartigan's K-Means program. Individual plants were used as operational taxonomic units (OTU's) and a total data set of 207 OTU's were analyzed. The program executed ten internal iterations and computed a maximum of ten clusters using zero as a starting point. Flower color was entered as ordinal data from 0 to 5 for yellow (white to yellow) and purple (white to purple). A discriminant analysis of the data set was generated by use of the SYSTAT DISCRIM program. Finally a tree diagram illustrating the relationships of the populations studied was generated using euclidean distances and single linkage methods (SYSTAT JOIN). Mean population values were entered for each character.

*Flavonoid Studies.* Petals, sepals, and stigmas from 10–20 individuals were collected from ten of the study populations and flavonoids were extracted in acidified methanol for 36–48 hours under refrigeration (Parks 1965). Approximately 20  $\mu$ m of extract was applied to Analtech Avicel F cellulose thin layer plates for simultaneous development. TBA was used for both directions (6:2:1 and 3:1:1 respectively). The dried plates were observed under long- and shortwave UV light and marked for pigment spots. Spectral data of pigment spots were obtained by removing the spot from the plate



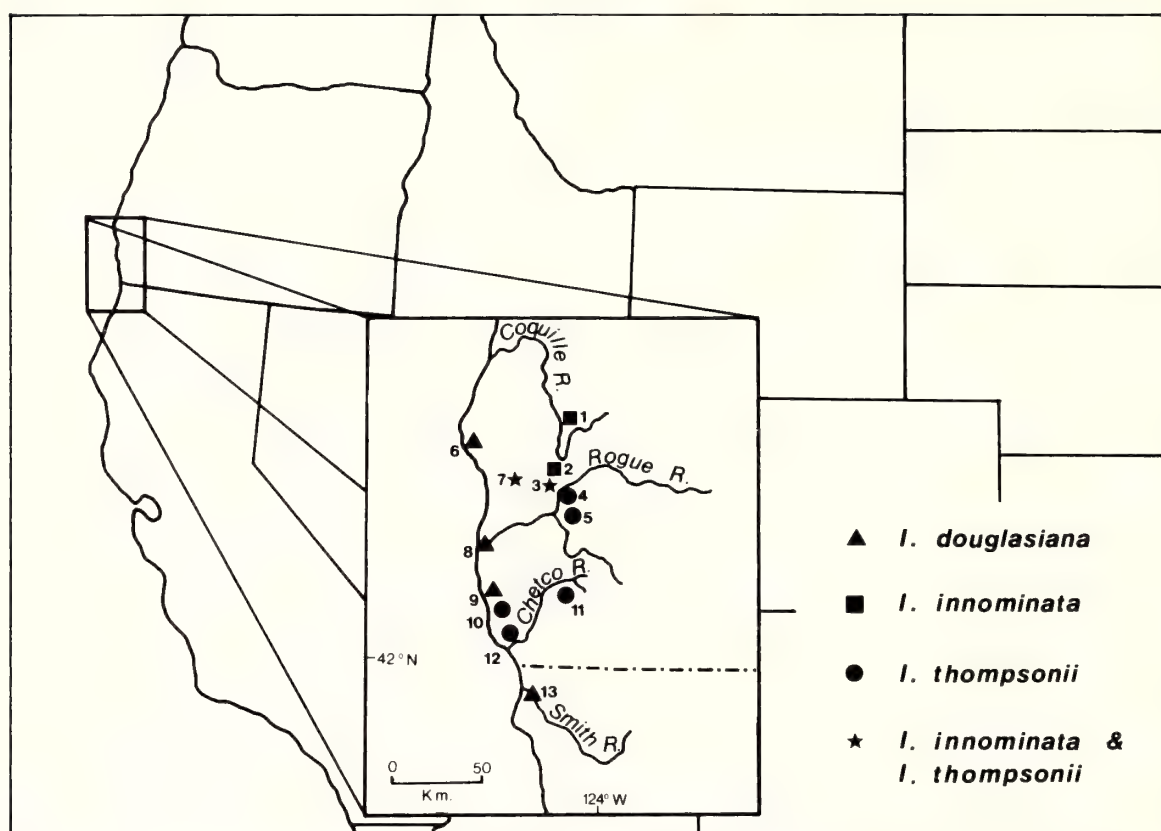


FIG. 1. Study populations of three *Iris* species from southwestern Oregon and northern California. 1. Daphne Grove. 2. Iron Mountain I. 3. Road 333. 4. Road 3400. 5. Road 3406. 6. Cape Blanco. 7. Iron Mountain II. 8. Champion Park. 9. Meyers Creek. 10. Carpenterville. 11. Snaketooth Road. 12. Chetco River. 13. Smith River.

and extracting the pigment in acidified methanol. A Beckman DU-7 spectrophotometer was used for gathering spectral data.

## RESULTS

*Numerical Studies.* Three clusters were found to be optimum, as the mean distance to cluster centers decreased by 42.3% with the formation of a third cluster but the mean distance only decreased by 2.0% when a fourth cluster was formed. *Iris douglasiana* was represented by Cape Blanco, Meyers Creek, Smith River, and Champion Park populations. Daphne Grove and Iron Mountain I populations formed a cluster representing *Iris innominata*. Carpenterville, Chetco River, Snaketooth Road, Road 3400, and Road 3406 formed the third cluster which identifies populations of *I. thompsonii*. Iron Mountain II and Road 333 represent mixed populations with members classified as *I. innominata* or *I. thompsonii*. *Iris innominata* has a more compact cluster (mean distance to cluster center 0.33), indicating that this species is more homogeneous than *I. douglasiana* (mean distance 0.56) and *I. thompsonii* (mean distance 0.45). Mean character values ( $\pm$  SE) for the three species are given in Table 2.

The discriminant analysis verified the classification of the thirteen



TABLE 2. MEAN VALUES ( $\pm$  SE) OF NUMERICAL CHARACTERS AND RATIOS FOR THREE *IRIS* SPECIES FROM SOUTHWESTERN OREGON AND NORTHERN CALIFORNIA. <sup>1</sup>Measurements are in mm. <sup>2</sup>Not used in numerical programs.

|                          | <i>I. douglasiana</i> | <i>I. innominata</i> | <i>I. thompsonii</i> |
|--------------------------|-----------------------|----------------------|----------------------|
| Characters <sup>1</sup>  |                       |                      |                      |
| Yellow flowers           | 0.1 $\pm$ 0.06        | 4.9 $\pm$ 0.03       | 0.0 $\pm$ 0.03       |
| Purple flowers           | 4.7 $\pm$ 0.09        | 0.0 $\pm$ 0.00       | 4.7 $\pm$ 0.10       |
| Number of leaves         | 1.9 $\pm$ 0.07        | 2.1 $\pm$ 0.08       | 2.1 $\pm$ 0.11       |
| Leaf width               | 1.3 $\pm$ 0.02        | 0.5 $\pm$ 0.01       | 0.4 $\pm$ 0.00       |
| Number of flowers        | 3.3 $\pm$ 0.89        | 1.0 $\pm$ 0.00       | 1.1 $\pm$ 0.05       |
| Stem length <sup>2</sup> | 19.0 $\pm$ 1.11       | 12.6 $\pm$ 0.58      | 16.5 $\pm$ 0.81      |
| Bract length             | 7.7 $\pm$ 0.15        | 4.2 $\pm$ 0.08       | 4.5 $\pm$ 0.09       |
| Bract width              | 1.7 $\pm$ 0.03        | 1.1 $\pm$ 0.02       | 1.2 $\pm$ 0.04       |
| Petal length             | 5.7 $\pm$ 0.08        | 4.3 $\pm$ 0.05       | 4.7 $\pm$ 0.08       |
| Petal width              | 1.4 $\pm$ 0.03        | 1.0 $\pm$ 0.01       | 1.0 $\pm$ 0.02       |
| Sepal length             | 6.3 $\pm$ 0.09        | 4.9 $\pm$ 0.06       | 5.2 $\pm$ 0.10       |
| Sepal width              | 2.4 $\pm$ 0.05        | 1.9 $\pm$ 0.03       | 2.0 $\pm$ 0.05       |
| Stigma length            | 4.3 $\pm$ 0.06        | 3.1 $\pm$ 0.03       | 3.4 $\pm$ 0.05       |
| Stigma width             | 1.3 $\pm$ 0.02        | 1.1 $\pm$ 0.02       | 1.1 $\pm$ 0.04       |
| Stigma lobe length       | 1.3 $\pm$ 0.02        | 1.1 $\pm$ 0.00       | 1.2 $\pm$ 0.01       |
| Peduncle length          | 2.8 $\pm$ 0.12        | 0.8 $\pm$ 0.05       | 0.8 $\pm$ 0.05       |
| Perianth tube length     | 1.6 $\pm$ 0.02        | 2.1 $\pm$ 0.03       | 2.4 $\pm$ 0.05       |
| Ratios <sup>2</sup>      |                       |                      |                      |
| Bract length/width       | 4.7 $\pm$ 0.13        | 3.7 $\pm$ 0.09       | 3.8 $\pm$ 0.13       |
| Petal length/width       | 4.3 $\pm$ 0.10        | 4.4 $\pm$ 0.06       | 4.8 $\pm$ 0.11       |
| Sepal length/width       | 2.7 $\pm$ 0.03        | 2.6 $\pm$ 0.03       | 2.7 $\pm$ 0.05       |
| Stigma length/width      | 3.6 $\pm$ 0.07        | 2.9 $\pm$ 0.06       | 3.2 $\pm$ 0.09       |

populations into three groups (Fig. 2). Again, Iron Mt. II and Road 333 were found to be mixed populations with both *I. innominata* and *I. thompsonii* present. The classification of the thirteen populations into three groups was found to be highly significant (F-statistic 336.9). The functions computed were found to be closely correlated to the groups discriminated as shown by the large values of the canonical correlations (0.988 and 0.976). Discriminant values show patterns similar to results from the cluster analysis, with *I. innominata* having the smallest range for discriminant values. Two populations, Snaketooth Road and Champion Park, had OTU's that were some distance from the group center (Fig. 2, a and b, respectively). These OTU's are considered to be variants within these populations. These three OTU's are not candidates for current hybridization, as the two populations from which they were collected are not presently sympatric with populations of other species and past hybridizations are not suspected as the other OTU's analyzed from the populations do not show evidence of intermediate character states (27 and 17 OTU's were analyzed from the Snaketooth and Champion Park populations, respectively).



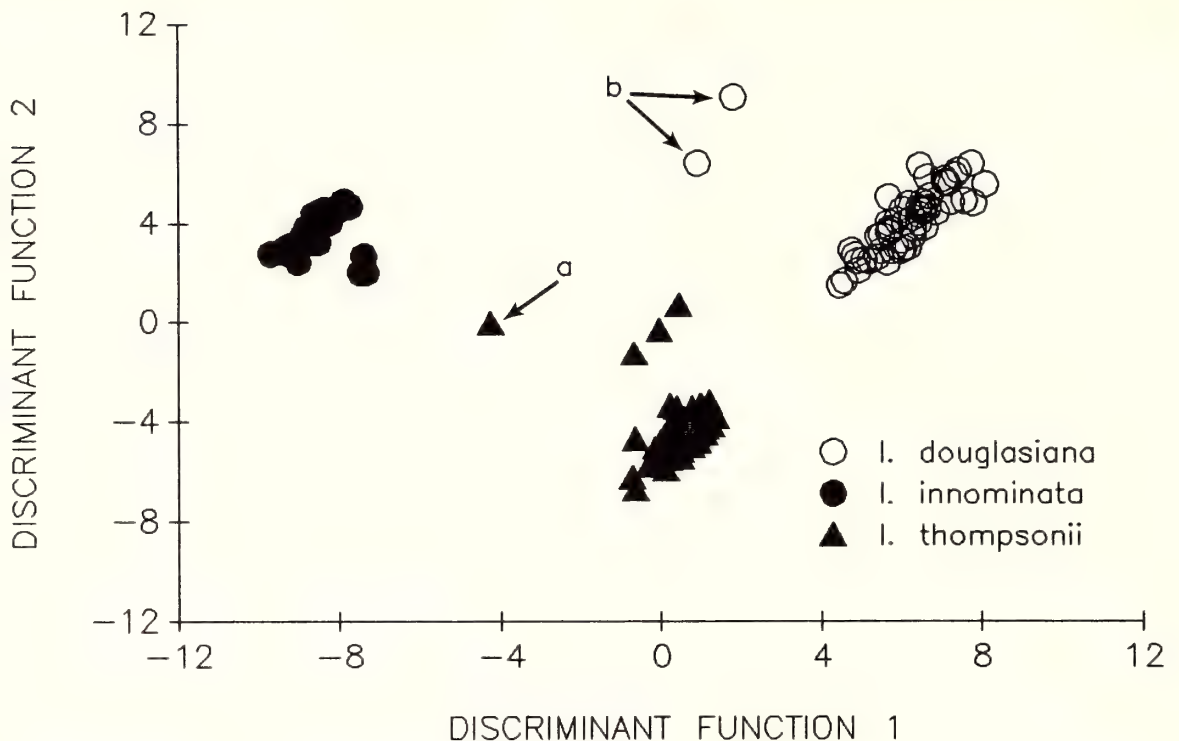


FIG. 2. Separation of three species of *Iris* from southwestern Oregon and northern California using SYSTAT DISCRIM. a. OTU from Snaketooth Road. b. OTU's from Champion Park.

Figure 3 illustrates the relationships of the populations studied. Based on discriminant and clustering data, the Iron Mt. and Rd. 333 populations have been subdivided into Iron Mt. II-i, Iron Mt. II-t, Road 333-i, and Road 333-t indicating the species present.

*Flavonoid Studies.* Fourteen flavonoid spots that are characteristic for the three species were resolved from the populations studied (Table 3). Four flavonoids are common to all three species. Pigment spots D5–D7 were found only in populations of *I. douglasiana*; I3, I4, and I7 in populations of *I. innominata*; and T1 and T2 in *I. thompsonii*. Two flavonoid spots (I1 and Y2) were found in populations of *I. innominata* and *I. thompsonii* but not in populations of *I. douglasiana*. Several additional flavonoid spots were also found in one or sometimes two populations of a taxon but are not considered here as they contribute no additional information. As indicated in Table 3, Champion Park did not contain two of the flavonoid spots that were present in other *I. douglasiana* populations studied.

## DISCUSSION

Foster (1937) recognized three species in his survey and cited differences in flower color, perianth tube length, shape of perianth and spathes (bracts), and nature of cauline leaves as support for the recognition of *I. thompsonii* as a species separate from *I. innominata*.



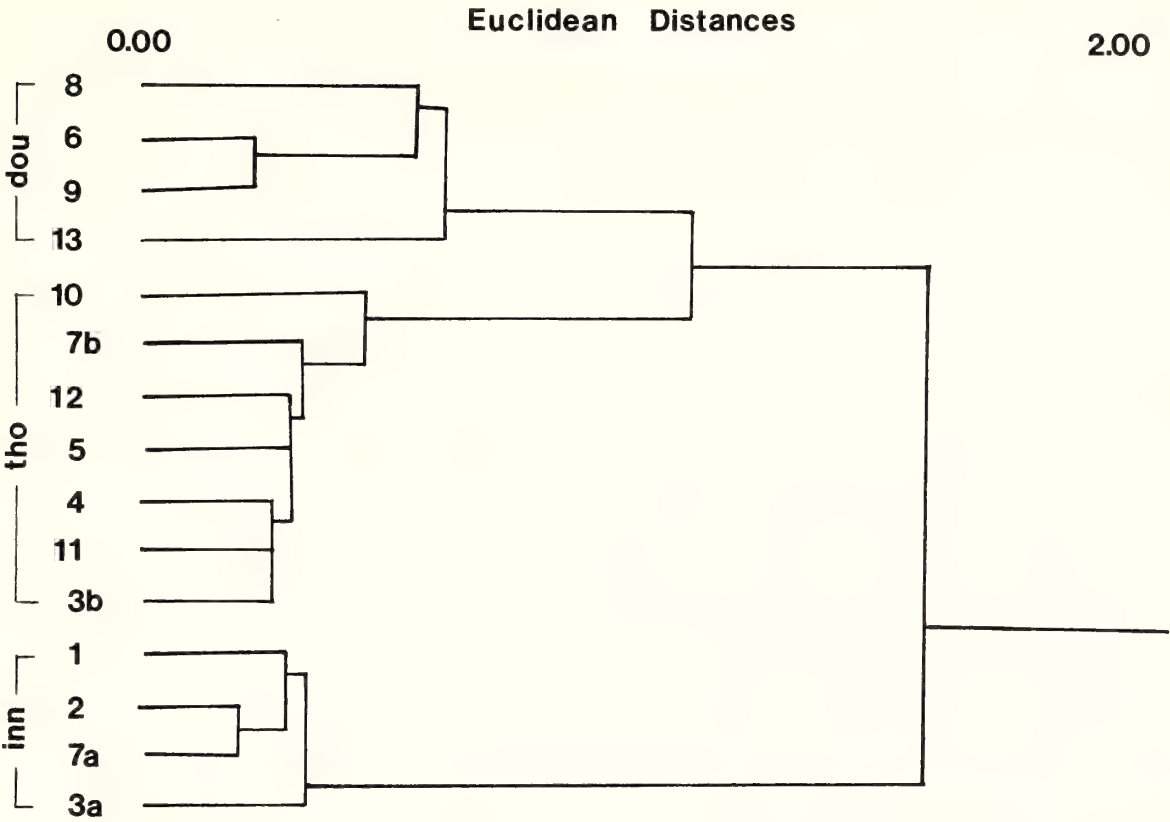


FIG. 3. Tree diagram of populations of three *Iris* species from southwestern Oregon and northern California using morphological characters and the SYSTAT JOIN algorithm. 1. Daphne Grove. 2. Iron Mountain I. 3a. Road 333-i. 3b. Road 333-t. 4. Road 3400. 5. Road 3406. 6. Cape Blanco. 7a. Iron Mountain II-i. 7b. Iron Mountain II-t. 8. Champion Park. 9. Meyers Creek. 10. Carpenterville. 11. Snaketooth Road. 12. Chetco River. 13. Smith River.

He indicated that the perianth tube of *I. thompsonii* was shorter than that of *I. innominata*. During this study it was determined that the perianth tube of *I. thompsonii* was longer than that of *I. innominata* and *I. douglasiana*. Foster's description was based on one herbarium specimen, which may account for the discrepancy between this study and his findings. During this study the petals, sepals, and stigmas of *I. thompsonii* were found to be longer relative to their width when compared to *I. innominata* (Table 2), supporting Foster's assertion that differences in perianth shape occur. Lenz (1958), in his revision of the Pacific Coast iris, considered *I. douglasiana* and *I. innominata* to be species, but proposed that *I. thompsonii* be retained within the yellow-flowered *I. innominata*. He considered the cream to purple *I. thompsonii* to be a color form or in some populations a hybrid between this species and the purple-flowered *I. douglasiana*. Clarkson (1962) concluded that *I. thompsonii* was of hybrid origin and occupied a habitat intermediate to *I. douglasiana* and *I. innominata*. He found that *I. innominata* was restricted to serpentine sites whereas *I. douglasiana* was found on non-serpentine sites. He postulated that *I. thompsonii* was able to



TABLE 3. TAXONOMIC DISTRIBUTION OF FLAVONOID SPOTS IN FLORAL PARTS OF THREE *IRIS* SPECIES FROM SOUTHWESTERN OREGON AND NORTHERN CALIFORNIA. <sup>1</sup>Champion Park population lacked pigment spots D5 and D6.

| Species                            | Flavonoid spots |    |    |    |    |    |    |    |    |    |    |    |    |    |
|------------------------------------|-----------------|----|----|----|----|----|----|----|----|----|----|----|----|----|
|                                    | D1              | D2 | D3 | D4 | D5 | D6 | D7 | I1 | I3 | I4 | I7 | Y2 | T1 | T2 |
| <i>I. innominata</i>               | X               | X  | X  | X  | —  | —  | —  | X  | X  | X  | X  | X  | —  | —  |
| <i>I. douglasiana</i> <sup>1</sup> | X               | X  | X  | X  | X  | X  | X  | —  | —  | —  | —  | —  | —  | —  |
| <i>I. thompsonii</i>               | X               | X  | X  | X  | —  | —  | —  | X  | —  | —  | —  | X  | X  | X  |

colonize sites intermediate to the habitats of the parental species. His study suggested that *I. thompsonii* should be recognized as a separate taxon although he did not favor species status for any of the three taxa. Clarkson had earlier proposed reducing all of the six Oregon members of the series to subspecific rank under *I. tenax*, the most widespread of the Oregon species (Clarkson 1959). He based this reduction in status on lack of “cytological barriers” and the presence of natural hybrids. His taxonomic treatment has not been generally accepted.

During field work it was found that *I. douglasiana* is restricted to a narrow band within 2 kilometers of the ocean (Fig. 1), usually on grassy headlands and in pastures. It is associated with well developed soils at most sites (the Meyers Creek population is adjacent to a large serpentine outcrop). *Iris innominata* was found to have a limited distribution in the northern portion of the study area. It occurred at higher elevations on rocky, sparsely vegetated sites. A greater portion of the study area was occupied by *I. thompsonii*. It was found in light shade on both grassy and gravelly sites. The three species are commonly found along roadsides, possibly because of the openness of such habitats. Although soil type was not ascertained during this study, observation of the soils and associated communities generally supports Clarkson’s opinion that *I. innominata* is found on serpentine sites, *I. douglasiana* is found on non-serpentine sites, and *I. thompsonii* occupies intermediate sites.

Numerical data indicate that *I. innominata* is the most homogeneous species, *I. douglasiana* is the most variable of the species, and *I. thompsonii* has an intermediate level of variability. The level of variation is expressed both overall (Fig. 2 and average distance-to-cluster center) and in individual characters (Table 2) for the three species. Variation in flower color has been problematic in the taxonomy of these species (Lenz 1958, 1959a; Clarkson 1959). In the present study, it was found that *I. innominata* has butter yellow flowers and shows little variation in flower color, whereas both *I. thompsonii* and *I. douglasiana* (mainly purple-flowered species) show



variation in flower color. Plants with white, cream, grey, red, blue, and lavender flowers occur in some populations of *I. thompsonii* whereas plants with cream, blue, and lavender flowers occur in some *I. douglasiana* populations.

Hybridization among members of the series *Californicae* has been cited by several workers. Foster (1937) in his survey of the North American species of *Iris* cited the importance of crossing on speciation within the group. He suggested that the series is composed of several species-complexes. He considered *I. innominata* and *I. thompsonii* to be clearly allied and possibly best placed in a complex with *I. douglasiana*, *I. bracteata*, and *I. purdyi*. Due to geographical and morphological considerations, he did not feel that such a complex could be clearly delineated. Smith and Clarkson (1956) examined cytology and embryo development in artificial crosses between species within the series. They found that fertile hybrids were produced between all crosses except *I. tenuis*. *Iris tenuis* has been transferred to the subsection *Evansia* (Lenz 1959b) largely due to chromosome studies (*I. tenuis* has  $2n=28$  chromosome numbers whereas all of the *Californicae* are uniformly  $2n=40$ ). Morphological characters (Lenz 1959a; Clarkson 1959, 1962; Clarkson and Thompson 1961) and chemical and morphological characters (Carter and Brehm 1969) have been analyzed in naturally occurring hybrids within the series. These studies established that fertile hybrids were found in nature and that hybrids were intermediate except in flower color. The studies by Lenz, Clarkson, and Clarkson and Thompson included *I. innominata*, *I. douglasiana*, and *I. thompsonii*. Each of these studies concluded, based upon the intermediate morphology and variable flower color, that *I. thompsonii* was a probable hybrid of *I. douglasiana* and *I. innominata*.

The present study does not provide clear support for a hybrid origin for *I. thompsonii*. In most characters it is intermediate to the putative parents. However, it is smaller in leaf width and has a longer perianth tube than either parent (Table 2). Perianth tube length was found to be 150% as long as in *I. douglasiana* and 114% as long as in *I. innominata*. Perianth tube length is considered important in the taxonomy of the series. The series is often subdivided into species with long (greater than three cm), short (less than one cm), and intermediate (1.5–2.5 cm) perianth tubes. The three species investigated in this study consist of the entire intermediate group.

Results from numerical methods placed *I. thompsonii* closest to *I. douglasiana* (Figs. 2 and 3). Flavonoid data indicate that it may be close to *I. innominata*, as it shares two flavonoid pigments with that species that are not found in *I. douglasiana* (Table 3). The analysis of flavonoids for a diploid hybrid is predicted to result in a pigment profile intermediate to the two parents where pigments



common to both parents would be present but not all pigments would be represented. Such profiles have been well documented in natural hybrids of the genus *Baptisia* and summarized by Alston (1967). In the series *Californicae*, intermediate flavonoid profiles have been documented for natural hybrids of *I. tenax* and *I. chrysophylla* (Carter and Brehm 1969). If *I. thompsonii* is of hybrid origin, sufficient time may have elapsed for the development of a unique flavonoid pattern.

Although the potential for hybridization has been demonstrated by earlier studies (Smith and Clarkson 1956), no evidence of recent hybridization was found. In populations where the two species were found growing together (Iron Mt. II and Road 333), intermediate plants were not found. Hybridization events may be rare or gene flow may not be facilitated between hybrids and other individuals. Differences were found in phenology, with *I. thompsonii* populations blooming generally in April and May, *I. innominata* blooming in late May and June, and *I. douglasiana* blooming in June and July. Differences in habitat preferences and perianth tube length have been discussed above. These factors may also serve to reduce gene flow among the species.

In summary, this study found that three species are present within the study area: *I. douglasiana*, *I. innominata*, and *I. thompsonii*. Of these three species, the yellow-flowered *I. innominata* is the most homogeneous species and is limited in distribution. Purple-flowered *I. douglasiana* and *I. thompsonii* are more variable both in flower color and other characters. Although neither of these would be considered a widespread species, both have larger distributions than *I. innominata*. The larger overall size and greater number of flowers per inflorescence easily distinguishes *I. douglasiana* from *I. innominata* and *I. thompsonii*. The purple flowers and longer perianth tube, bracts, and perianth parts distinguish *I. thompsonii* from *I. innominata* (Table 2). Differences in interspecific variation were not demonstrated. Numerical data indicate that *I. douglasiana* and *I. thompsonii* are more closely allied than *I. innominata* is to either of the two species. However, flavonoid data argue for a closer relationship between *I. innominata* and *I. thompsonii*. Although clearly *I. thompsonii* should not be considered a color variant of *I. innominata* or an occasionally occurring hybrid between *I. douglasiana* and *I. innominata*, the origin of the species is more difficult to determine. The morphological and flavonoid data do not support the currently accepted hypothesis of a recent hybrid origin for the species, although speciation following a hybrid event is a possibility. The origin of *I. thompsonii* may be resolved with further studies involving different techniques and study of other members within the series.



## ACKNOWLEDGMENTS

This paper is dedicated to the memory of Q. D. Clarkson, who encouraged the initiation of this project. A grant from the Portland State University Research and Publications Committee provided partial funding for the UV spectral analysis.

## LITERATURE CITED

- ALSTON, R. E. 1967. Biochemical systematics. Pp. 197–299 in T. Dobzhansky, M. K. Hecht, and W. C. Steere (eds.), *Evolutionary biology*, Vol. 1. Appleton-Century-Crofts, New York.
- CARTER, L. C. and B. G. BREHM. 1969. Chemical and morphological analysis of introgressive hybridization between *Iris tenax* and *I. chrysophylla*. *Brittonia* 21: 44–54.
- CLARKSON, Q. D. 1959. Field studies of natural hybridization in the Oregon species of *Iris* L. subsection *Californicae* Diels. *Madroño* 15:115–122.
- . 1962. Ecological factors in the hybridization of *Iris tenax douglasiana* (Herbert) Clarkson *Iris tenax innominata* (Henders.) Clarkson. *Northwest Science* 36:59–64.
- and D. I. THOMPSON. 1961. Analysis of a hybrid *Iris* near Elmira, Lane County, Oregon. *Northwest Science* 35:27–31.
- FOSTER, R. C. 1937. A cyto-taxonomic survey of the North American species of *Iris*. *Contr. Gray Herb.* 119:1–82.
- KRUCKEBERG, A. R. 1954. III. Plant species in relation to serpentine soils. *Ecology* 35:267–274.
- . 1986. An essay: the stimulus of unusual geologies for plant speciation. *Syst. Bot.* 11:455–463.
- LENZ, L. 1958. A revision of the Pacific Coast irises. *Aliso* 4:1–72.
- . 1959a. Hybridization and speciation in the Pacific Coast irises. *Aliso* 4: 237–309.
- . 1959b. *Iris tenuis* S. Wats., a new transfer to the subsection *Evansia*. *Aliso* 4:311–319.
- PARKS, C. R. 1965. Floral pigmentation studies in the genus *Gossypium*. I. Species specific pigmentation patterns. *Amer. J. Bot.* 52:309–316.
- SMITH, F. H. and Q. D. CLARKSON. 1956. Cytological studies of interspecific hybridization in *Iris*, subsection *Californicae*. *Amer. J. Bot.* 43:582–588.
- WALKER, R. B. 1954. II. Factors affecting plant growth on serpentine soils. *Ecology* 35:259–266.

(Received 16 Jun 1989; revision accepted 8 Nov 1989.)



# COMMENTS ON SOUTHWESTERN UNITED STATES *EVOLVULUS* AND *IPOMOEA* (CONVOLVULACEAE)

DANIEL F. AUSTIN

Department of Biological Sciences, Florida Atlantic University,  
Boca Raton, FL 33431

## ABSTRACT

*Evolvulus alsinoides* and *E. arizonicus* have historically been difficult to distinguish. Most specimens of these two taxa may be identified by corolla size; all specimens in this region by sepal size. Typification of *E. arizonicus* is discussed, and a lectotype chosen. The name *Ipomoea hirsutula* has been a mixed concept applied to two species in publications for a number of years. Proper names of these species (*Ipomoea hederacea* and *I. purpurea*), their traits, and ways of distinguishing them are discussed.

## RESÚMEN

*Evolvulus alsinoides* y *E. arizonicus* historicamente han sido difíciles de separar. La mayoría de las muestras de herbario de estas dos especies pueden distinguirse por el tamaño de la corola. Todas las muestras del sudoeste de los Estados Unidos pueden distinguirse por el tamaño de los sepalos. Tipificación de *E. arizonicus* se discute, y se selecciona un lectotipo. El nombre *Ipomoea hirsutula* ha sido un concepto mixto que fué aplicado a dos especies en las publicaciones en el pasado. Los nombres correctos para estas dos especies son *Ipomoea hederacea* y *I. purpurea*. Se presentan sus características y los modos de distinguirlas.

## EVOLVULUS L.

*Evolvulus* has within it a complex of species allied with *E. alsinoides* that remains confusing to all who have studied them recently (Ooststroom 1934; Kearney and Peebles 1942; Kearney et al. 1951, 1960; Shreve and Wiggins 1964; Martin and Hutchins 1981). The only revision of the complex was made by Ooststroom (1934). In this revision, based entirely on herbarium material, Ooststroom recognized many varieties of several species. Most of the varieties are, in my opinion, manifestations of phenotypic plasticity and are unworthy of formal taxonomic rank. Still, there is need for study of the *E. alsinoides* complex to determine the source of the variation.

Two characters have been used to distinguish *E. alsinoides* from *E. arizonicus*—corolla size and pubescence type. According to Ooststroom (1934), *E. alsinoides* has corollas 5.5–7 mm wide, and *E. arizonicus* has corollas up to 16 mm wide (no minimum was given). Pubescence of *E. alsinoides* is characterized by appressed and spreading trichomes on the stems (Ooststroom 1934). *Evolvulus arizonicus* var. *arizonicus* has only spreading trichomes, although *E. arizonicus* var. *laetus* has appressed and spreading trichomes like



TABLE 1. COMPARISON OF COROLLA SIZES IN LIVING AND HERBARIUM SPECIMENS OF *EVOLVULUS ALSINOIDES* AND *E. ARIZONICUS*.

| <i>E. alsinoides</i>            | <i>E. arizonicus</i> |
|---------------------------------|----------------------|
| Corollas of herbarium specimens |                      |
| Number = 25                     | Number = 89          |
| Range = 5–10 mm                 | Range = 10–19 mm     |
| Mean = 7.1 mm                   | Mean = 12.89 mm      |
| Mode = 7 mm                     | Mode = 12 mm         |
| Corollas of living specimens    |                      |
| Number = 133                    | Number = 138         |
| Range = 6–10 mm                 | Range = 12–20 mm     |
| Mean = 8.26 mm                  | Mean = 17.28 mm      |
| Mode = 8 mm                     | Mode = 19 mm         |

*E. alsinoides*. Subsequent authors have varied in their interpretations of the corolla sizes and, to some extent, pubescence (Wooten and Standley 1915; Tidestrom and Kittell 1941; Kearney and Peebles 1942, 1951, 1960; Shreve and Wiggins 1964; Martin and Hutchins 1981).

Since the delimitation of the two species has been based largely on corolla sizes in the past, measurements were made of specimens with corollas in ARIZ. I also studied the pubescence on these specimens. Later I used the 1989 fall flowering period in Arizona to make corolla measurements and examine pubescence on living specimens from several parts of the range.

In the ARIZ sample, there is a continuous range of corolla sizes from 5 to 19 mm wide (Table 1). Field measurements, however, show that living corollas of *E. alsinoides* range from 6–10 mm wide, and those of *E. arizonicus* range from 12–20 mm wide. Thus, the two species may normally be separated by corolla size at least on living specimens. The task becomes more difficult, and at times impossible, on herbarium material. Apparently the difficulty results from two components.

The most important component of overlap in the two species is found where they occur sympatrically or parapatrically. In the samples made during 1989 there was complete geographic separation except in one site. At this locality (Redington Pass, Pima Co., AZ) the two species were sympatric and intermixed, and a few plants showed intermediate corolla sizes.

A second component of potential misidentification is corolla shrinkage. In living specimens studied in 1989, the corollas shrunk by as much as 2–3 mm as they wilted. When the corollas of *E. arizonicus* are on the small end of the size range, such shrinkage would bring them down into the *E. alsinoides* range. Failure to press the specimens immediately also allows them to wilt and shrink.



All of the specimens examined in ARIZ had appressed pubescence in the large-flowered forms, but some spreading trichomes on plants with the smaller end of the corolla size range. I observed the same situation in living plants.

Both the intermediate flower sizes and the sharing, on some specimens, of pubescence traits may indicate a hybrid origin. Specimens with intermediate flower sizes and pubescence are those previously separated as *E. arizonicus* var. *laetus*. In the field and the herbarium these specimens have more traits of *E. arizonicus* than *E. alsinoides*. For this reason, I continue to include them within that species.

Because corolla size and pubescence are unreliable characters for determination of intermediate specimens, another trait is needed. I found that sepal length measurements work well. Ooststroom (1934) listed this trait, but did not indicate that it might be used to separate taxa. The following key summarizes the distinctions between the species.

- a. Flowering sepals 2–2.5 mm long; corolla (5–)7–10 mm wide; stems with appressed and long spreading trichomes. .... *E. alsinoides*
- a' Flowering sepals 3–3.5 mm long; corolla (10–)12–22 mm wide; stems with appressed trichomes, rarely with spreading trichomes. .... *E. arizonicus*

#### NOMENCLATURAL SUMMARY

1. *EVOLVULUS ALSINOIDES* L. var. *ANGUSTIFOLIA* Torrey, Bot. Mex. Bound. 150. 1858. TYPE: Texas. Brewster Co. Near the Grand Canyon of the Rio Grande. August. *Parry s.n.* (GH, not found; US, not found; NY, not found).
- E. acapulcensis* Willd. ex Roemer & Schultes, Syst. Veg. 6:199. 1820; *E. alsinoides* var. *acapulcensis* (Willd.) Ooststr., Meded. Bot. Mus. Herb. Rijks Univ. Utrecht 14:34. 1934. Type: Mexico. Guerrero. near Acapulco. herb. *Willdenow 6128* (B, not seen). Interpretation based on annotations by Ooststroom who saw the type.

Shinners (1970) was apparently the first to point out that this was the correct name for the plants in the Trans-Pecos area of Texas. The same variant occurs sparingly in New Mexico and occasionally in Arizona.

*Representative specimens.* USA. Arizona: Cochise Co.: Huachuca Mts., Ramsey Canyon, *Toolin 971* and *Yatskievych 80-377* (ARIZ); Pima Co.: Rincon Mts., Manning Trail, *Blumer 3326* (ARIZ); Pinal Co.: upper Oak Springs Canyon, *Anderson and Warren 210* (ARIZ); Santa Cruz Co.: Sycamore Canyon, Goodding Research Area, *Kaiser 764* (ARIZ). New Mexico: Dona Ana Co.: S end Organ Mts., Long Canyon, *Todsen 700802-3* (NMC). Texas: Terrell Co.: Sanderson,



*Crockatt 16; 77* (both NMC). Mexico. Chihuahua: N Ciudad Chihuahua, *Ward and Worthington 81-369* (NMC).

2. *EVOLVULUS ARIZONICUS* A. Gray, *Syn. Fl. N. Amer.* 2, 1:218. 1886.—TYPE: See discussion below. Ooststroom (1934, p. 74), selected the following collection as lectotype: (Mexico. Sonora, sandy plains near the U.S. (the label says Mexican) boundary, 30 Aug 1884, *C. G. Pringle s.n.*). He did not cite an herbarium; I have seen specimens of this collection in BR, K, P, U and US. Ooststroom did not cite a single specimen of this species from GH, and presumably saw none of the GH material of this species.

There are eight collections in GH that bear annotations in Gray's own hand, and four of these bear the printed label for "Syn. Fl. N. Amer." The Pringle collection cited by Ooststroom is not in GH, although it does exist at US, without Gray's annotation. There is no evidence that Gray saw the specimens in BR, K, P, or U since he did not annotate them nor did he cite the collection. Because there is no evidence that Ooststroom saw any of the original material used by Gray, I consider his action that of neotypification (Greuter et al. 1988, Art. 7.9). Because the specimen cited by Ooststroom seems to be a neotype selected when original type material was available, a superceding lectotype still must be chosen.

I select here the following specimen as lectotype: Mexico: Sonora: Sandy prairies, flws blue, Sep 1857, *G. Thurber 1023* (specimen in GH!, annotated by Gray and bearing his "Syn. Fl. N. Amer." label). A second sheet, bearing three collections, was also annotated and labeled by Gray: Arizona: S. Pedro R., Jun, *E. K. Smith s.n.* (GH!, fl); Arizona, without location, 1873, *Dr. Loud 151-a* [spelling?] (GH!, fl and fr); Arizona: Camp Grant, 4753 feet, Jul 1874, *Dr. Rothrock 376* (GH!, buds).

- E. arizonicus* A. Gray var. *laetus* (A. Gray) Ooststr., *Meded. Bot. Mus. Herb. Rijks Univ. Utrecht* 14:76. 1934.—*E. laetus* A. Gray, *Proc. Amer. Acad. Arts* 17:228. 1882.—TYPE: Arizona, mesas and foot-hills of the Santa Rita Mountains. 6 May 1881. *C. G. Pringle* (holotype GH!; isotypes, F!, US!).

*Representative specimens.* USA. Arizona: Cochise Co.: Dragoon Mts., S jct Triangle T road with I-10, *Reeder and Reeder 7897* (ARIZ); Gila Co.: Mazatzal Mts., Collom Camp, *Collom 6973* (ARIZ); Graham Co.: Pinaleno Mts., Jesus Canyon, *Shreve 5278* (ARIZ); Greenlee Co.: 2 mi N Clifton, *Maguire et al. 11818* (ARIZ); Pima Co.: near jct FSR505 and FSR485, *McLaughlin 3416* (ARIZ); Pinal Co.: Oracle, *Thornber s.n.* (ARIZ); Santa Cruz Co.: Sta. Rita



Mts., Sta. Rita Research Reserve, *Haskell s.n.* (ARIZ); Yavapai Co.: upper Weaver Creek, *Butterwick and Hillyard 6878* (ARIZ, ASU); Unknown County: w/o locality, *Griffiths 1960* (ARIZ). New Mexico: Dona Ana Co.: Organ Mts., Parker's Well, 19 Jul 1901, *Wooton s.n.* (NMC); Hidalgo Co.: SW corner of the county, Guadalupe Canon, vic. of Hadley Ranch, *Spellenberg and Repass 5387* (NMC).

### IPOMOEA L.

Since *Ipomoea hirsutula* Jacq. f. (1811) was published, most people who have used the name, either in synonymy or as an accepted name, have misapplied it (e.g., Wooton and Standley 1915; Tidestrom and Kittell 1941; Kearney and Peebles 1942; Kearney et al. 1951, 1960; Shreve and Wiggins 1964; Lehr 1978; Martin and Hutchins 1981). I have not attempted to determine exactly when this trend began in the southwestern United States, but it has been going on since near the turn of the century. The name was not used by Gray (1886), but it was used by House (1908) and by Wooton and Standley (1915). Examination of the keys published and the determinations on specimens used by previous authors indicates that they had a confused concept of the species. Indeed, previous authors included two species in their concept of *I. hirsutula* (*I. hederacea* and *I. purpurea*), and similar confusion of the species they misidentified dates back to Linnaeus. Confusion has persisted even though the problem has been repeatedly summarized (Verdcourt 1957, 1958; O'Donnell 1959; Shinnars 1965; Austin 1986). The name *I. hirsutula* Jacq. f. should not be used as the correct name for any plant since it is a synonym of *I. purpurea* (L.) Roth (Austin 1986).

The source of confusion concerning these plants arose from the use of a variable leaf character. Historically "*I. hirsutula*" has been separated from "*I. purpurea*" by whether or not the leaves were lobed or entire (Wooton and Standley 1915; Tidestrom and Kittell 1941; Kearney and Peebles 1942; Kearney et al. 1951, 1960; Shreve and Wiggins 1964; Martin and Hutchins 1981). Thus, the name "*I. purpurea*" came to be applied to entire-leaved specimens of *I. hederacea* and *I. purpurea*, and "*I. hirsutula*" was applied to lobed-leaved specimens of the same two species. This trait will not separate species since a single plant of either species may have entire and lobed leaves.

The following key, figure, review of nomenclature, and list of species and specimens indicates the proper placement in the southwestern United States. Even though *I. nil* has not been found in Arizona, the key also includes that species since it is similar to and easily confused with *I. hederacea*. *Ipomoea nil* occurs near the southwestern United States in the geographically adjacent and environmentally similar regions of Baja California, Sonora and Chihuahua



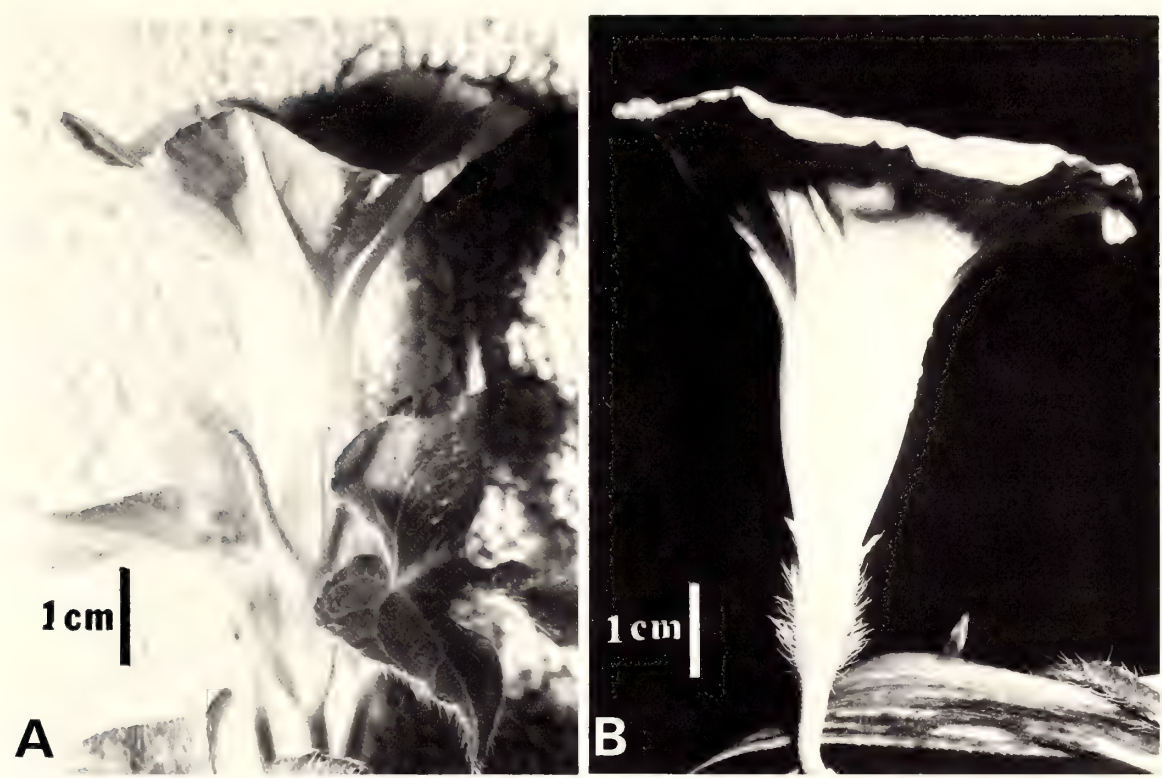


FIG. 1. A. Corolla and calyx of *Ipomoea hederacea*. B. Corolla and calyx of *I. purpurea*.

and extends south in Mexico into Jalisco, Hidalgo, Guerrero, and Oaxaca. The species is often cultivated, and may escape as it has in Texas, Louisiana, and Florida.

- a. Apices of sepals abruptly narrowing, shorter to slightly longer than body; sepals in flowering specimens 10–15 mm long; corollas 5–6 cm long (Fig. 1-B). . . . .  
..... *I. purpurea*
- a' Apices of sepals gradually narrowing, much longer than body; sepals in flowering specimens 12–35 mm long; corollas 2.5–8 cm long.
- b. Sepals 22–35 mm long, gradually narrowed, the long acute apices suberect, straight, scarcely spreading; corollas 5–8 cm long. . . . .  
..... *I. nil* (not known at present in AZ or NM, but in TX)
- b' Sepals 12–24 mm long, abruptly narrowed, the long, subacute apices strongly spreading or curved; corollas 2.5–5 cm long (Fig. 1-A). . . . . *I. hederacea*

NOMENCLATURAL SUMMARY AND NOTES ON TAXA

- 1. IPOMOEA HEDERACEA Jacq., Collect. 1:124. t. 36. 1787.—Type:  
Based on Dillenius, Hort. Elth. t. 80, fig. 92 (plate selected  
lectotype! by Verdcourt, 1957, 1958).  
*Ipomoea hirsutula* sensu authors, pro parte, non Jacq. f. (1811).  
For additional synonyms see Austin (1986).

The sepals on herbarium specimens from Arizona and nearby regions are not as strongly curved as are those on material from the southeastern United States. The curve is, however, evident in living material. Even on the plants from the southeastern United States,



the curve of the sepals is most easily seen in living plants, although it usually may be detected on preserved material also.

I suspect that *I. hederacea* and the similar *I. nil* may not be separate species; instead they are most likely subspecies of the latter species. *Ipomoea hederacea* is the temperate form (growing at high altitudes within the tropics), and *I. nil* the tropical, regardless of their taxonomic rank. Further studies are required to resolve the situation.

*Ipomoea hederacea* was first found in Arizona in 1891 (*Toumey s.n.* ARIZ), in New Mexico in 1895 (*Mulford 1088* NY), and in Texas in 1923 (Johnston 1959). This species was almost certainly introduced into the southwestern United States from the southeastern U.S. where it was originally endemic. Perhaps the species was introduced in cotton since it is a frequent weed in cotton fields (included by Parker 1972 as *I. hirsutula*, fig. 114).

*Representative specimens.* USA. Arizona: Cochise Co.: Sierra Vista, *McGill and Lehto 20454* (ASU); Coconino Co.: Sycamore Canyon Wilderness Area, *Pinkava et al. 5881* (ASU); Gila Co.: Kelvin, *Lehto and McGill 22364* (ASU); Graham Co.: Safford, *Bingham 1914* (ASU); Maricopa Co.: Tonto Forest Road 143, E Route 87, *Weber and Lehr 576* (DES); Pima Co.: Redington Rd, E of Tucson, *Austin and Austin 7596* (ASU); Pinal Co.: *Peebles 10255* (ARIZ); Santa Cruz Co.: Santa Rita Mts., *Thornber s.n.* (ARIZ); Yavapai Co.: Bloody Basin, Tangle Creek, *Blakeley 667* (DES); Yuma Co.: Cabeza Prieta Game Range at Montreal Well, *Munson s.n.*; Unknown County: S. Arizona, w/o locality, *Gentry s.n.* (ARIZ-273858). Texas: Jeff Davis Co.: lower Fern Canyon, *Warnock 809* (ARIZ). Mexico: Chihuahua: Sierra Madre Occidental, 82 mi W of Vieja Casas Grandes, *Tucker 2510* (ARIZ); Sonora: Alamas, Río Fuerte, *Gentry 2929* (ARIZ).

2. *IPOMOEA PURPUREA* (L.) Roth, Bot. Abh. 27. 1787.—*Convolvulus purpureus* L., Sp. Pl. ed. 2. 219. 1762. TYPE: Based on Dillenius, Hort. Elth. t. 84, fig. 97 (!lectotype by Verdcourt, 1957).

*Ipomoea hirsutula* Jacq. f., Eclog. Pl. Rariorum 1:65. t. 44. 1811.—

Type: No specimen located; the plate here chosen as lectotype. For additional synonyms see Austin (1986).

*Representative specimens.* USA. Arizona: Apache Co.: E of Ft. Apache, First Box Canyon, *Losper 16* (ASC); Cochise Co.: Chiricahua Mts., *Blumer 1892* (ARIZ); Gila Co.: Pinal Mts., Pioneer Pass Rec. Area, *Keil et al. 13329* (ASU); Graham Co.: US Hwy 70 at San Carlos River, *Pinkava et al. 15086* (ASU); Greenlee Co.: E Eagle Creek, 24 mi from Coronado Trail jct, *Gould and Robinson 5219* (ARIZ); Maricopa Co.: NE Phoenix, *Hubbs s.n.* (DES-26332); Navajo Co.: *Lehto 13951* (ASU); Pima Co.: Fresnal, Papago Indian Res., *Gouldman 107* (ARIZ); Santa Cruz Co.: Pena Blanca Lake,



*Lehto et al.* 17193 (ASU, DES); Yavapai Co.: Prescott, *Hurd* 2065 (ASC). New Mexico: Chaves Co.: Roswell, *Earle* 256 (TEX); Dona Ana Co.: Organ Mts., San Augustine Pass, *Worthington* 6635 (TEX); Grant Co.: Silver City, *Cole s.n.* (DES); Hidalgo Co.: road from Cloverdale to Douglas, *R. and M. Spellenberg* 3905 (ASU, NMC); Lincoln Co.: White Mts., *Wooton and Standley* 3631 (NMC); Luna Co.: Florida Mts., above Mahoney Park, *R. and M. Spellenberg* 6227 (NMC); Otero Co.: Sacramento Mts., Fresnal Canyon, *Ward and Soreng* 81-534 (NMC); San Miguel Co.: Pecos Canyon, Field Tract Camp Ground, *Austin and Austin* 7619 (ASU); Santa Fe Co.: Santa Fe, *Bartlett* 64 (NMC); Socorro Co.: Mogollon Mts., near "Grand Canyon" on the fork Gila, 19 Aug 1900. *Wooton s.n.* (NMC). Mexico: Chihuahua: Trompillo, Carretas, *White* 1112 (ARIZ); Sonora: Sierra Charuco, Río Mayo, *Gentry* 1709 (ARIZ).

#### ACKNOWLEDGMENTS

Thanks are extended to W. Hodgson (DES), C. T. Mason, Jr. (ARIZ), D. J. Pinkava (ASU), and J. M. Roeminger (ASC) for assistance during visits and for the opportunity to study specimens. G. W. Staples (GH) and D. H. Nicolson (US) examined labels on specimens and offered advice on typification. Thanks are due Paul Bamps (BR) and G. Ll. Lucas (K), who sent photocopies of their specimens, and to H. Halle and P. Morat (P) and Paul Maas (U), who sent loans of specimens. The fall season of 1989 was used to study these plants during a sabbatical at Arizona State University, Tempe.

#### LITERATURE CITED

- AUSTIN, D. F. 1986. Nomenclature of the *Ipomoea nil* complex (Convolvulaceae). *Taxon* 35:355–358.
- GRAY, A. 1886. Synoptical flora of North America. 2(1):207–224; 433–436. 2nd ed. Ivison, Blakeman, Taylor & Co., New York.
- GREUTER, W. ET AL. 1988. International code of botanical nomenclature. *Reg. Veg.* no. 118.
- HOUSE, H. D. 1908. The North American species of *Ipomoea*. *Ann. New York Acad. Sci.* 18:181–263.
- JACQUIN, J. F. 1811. *Eclogae plantarum rariorum*. Vienna. vol. 1: 63. plate 44 (part 5–6) Nov. 1813.
- JOHNSTON, M. C. 1959. Convolvulaceae in southern Coastal Texas. *Texas J. Sci.* 11:191–206.
- KEARNEY, T. H. and R. H. PEEBLES. 1942. Flowering plants and ferns of Arizona. *Misc. Publ. U.S. Dept. Agriculture* 423. pp. 702–711.
- , ———, and collaborators. 1951. *Arizona flora*. Univ. Calif. Press, Berkeley.
- , ———, and ———. 1960. *Arizona flora*, 2nd ed., with Supplement by J. T. Howell, E. McClintock, and collaborators. Univ. Calif. Press, Berkeley.
- LEHR, J. H. 1978. A catalogue of the flora of Arizona. Desert Botanical Garden, Phoenix.
- MARTIN, W. C. and C. R. HUTCHINS. 1981. A flora of New Mexico, Vol. 2. J. Cramer, Verlag, Germany.
- O'DONELL, C. A. 1959. Convolvulaceas argentinas. *Lilloa* 29:197–204.
- OOSTSTROOM, S. J. VAN. 1934. A monograph of the genus *Evolvulus*. *Meded. Bot. Mus. Herb. Rijks Univ. Utrecht* 14.



- PARKER, K. F. 1972. An illustrated guide to Arizona weeds. Univ. Arizona Press, Tucson.
- SHINNERS, L. H. 1965. Untypification for *Ipomoea nil* (L.) Roth. *Taxon* 14:231–234.
- . 1970. Convolvulaceae. Pp. 1241–1262 in D. S. Correll and M. C. Johnston (eds.), *Manual of the vascular plants of Texas*. Texas Research Foundation, Renner.
- SHREVE, F. and I. L. WIGGINS. 1964. *Vegetation and flora of the Sonoran Desert*, Vol. 2. Stanford Univ. Press, Stanford.
- TIDESTROM, I. and T. KITTELL. 1941. *Flora of Arizona and New Mexico*. Catholic University of America Press, Washington, D.C.
- VERDCOURT, B. 1957. The names of the morning glories cultivated and naturalised in East Africa. *Taxon* 6:231–233.
- . 1958. Notes on *Ipomoea* L. *Taxon* 7:84–85.
- . 1963. Convolvulaceae. Pp. 1–161 in C. E. Hubbard and E. Milne-Redhead (eds.), *Flora of Tropical East Africa*. Crown Agents for Oversea Governments, London.
- WOOTON, E. O. and P. C. STANDLEY. 1915. *Flora of New Mexico*. *Contr. U.S. Natl. Herb.* 19:514–519.

(Received 3 May 1989; revision accepted 9 Jan 1990.)



## PRESENT STATUS OF *AMBLYOLEPIS* (ASTERACEAE: HELIANTHEAE)

MARK W. BIERNER

Department of Biology, Southwest Texas State University,  
San Marcos, TX 78666

### ABSTRACT

*Amblyolepis*, a taxon of Texas and northeastern Mexico, is recognized as a monotypic genus in subtribe Gaillardiiinae, possibly most closely related to *Hymenoxys*. Although chromosome numbers of  $2n=18_{II}$ ,  $18_{II} + 1_I$ ,  $19_{II}$ ,  $19_{II} + 1_I$ , and  $20_{II}$  are reported, only one infrageneric taxon (*A. setigera*) is recognized, because there are no distinguishing morphologic characters that correlate with chromosome number. This taxonomic treatment takes into account all known morphologic, chemical, and cytologic data.

### RESUMEN

*Amblyolepis*, un taxón que se encuentra de Tejas y en el nordeste de México, es reconocido como un género monotípico en la subtribu Gaillardiiinae, que está posiblemente relacionada con *Hymenoxys*. Aunque los números de cromosomas de  $2n=18_{II}$ ,  $18_{II} + 1_I$ ,  $19_{II}$ ,  $19_{II} + 1_I$ , y  $20_{II}$  son reportados, solamente un taxón intragenérico (*A. setigera*) es reconocido ya que no hay características morfológicas que se correlacionen con el número de cromosomas. Este tratamiento taxonómico toma en cuenta todos los datos morfológicos, químicos y citológicos conocidos.

The monotypic genus *Amblyolepis* DC. consistently has been placed close to *Helenium* L. and *Gaillardia* Foug. (De Candolle 1836; Torrey and Gray 1842; Rydberg 1915; Correll and Johnston 1970; Robinson 1981), and at times it has even been treated as congeneric with *Helenium* (Bentham and Hooker 1873; Hoffmann 1894). Gray (1874, p. 201), however, responded to Bentham's (Bentham and Hooker 1873) reduction of *Amblyolepis* to a section of *Helenium* by stating, "I cannot at all accept the idea that *Amblyolepis* DC. belongs to this genus." He then itemized a number of differences between the two genera including vestiture, leaf shape, leaf punctuation, inner involuclral bract morphology, and achene and disc corolla morphology.

Indeed, there is no other taxon in subtribe Gaillardiiinae that has anything in common with *Amblyolepis* in regard to the above mentioned characters. Of particular note are the leaves, which lack impressed glands, the inner involuclral bracts, which are hyaline and resemble pappus scales, the achenes, which are very strongly 10-ribbed, and the disc corollas, which have long, slender tubes, funnelform throats, and relatively long, acuminate lobes.

Gray (1874, p. 201) also commented that *Amblyolepis* has "... somewhat the odor of *Melilotus* in drying." This undoubtedly is due



to the presence of coumarin (Herz and Bhat 1970), a compound that has not been reported from any other taxon in subtribe Gaillardinae. While this in itself is a notable chemical difference between *Amblyolepis* and the rest of the subtribe, it is probably more significant that Herz and Bhat (1970) were unable to detect any sesquiterpene lactones in *Amblyolepis setigera*, even though they were looking specifically for these compounds when they extracted some five kilograms of dried plant material. Sesquiterpene lactones are abundant in, and rather easily isolated from, other genera in the subtribe, especially *Helenium* and *Gaillardia* (Yoshioka et al. 1973; Herz 1977; Swain and Williams 1977; Seaman 1982).

Flavonoid chemistry of *Amblyolepis* is also quite distinct from that of *Helenium* and *Gaillardia*. *Amblyolepis* has been found to contain flavonols (Bierner 1979), while *Helenium* and *Gaillardia* have thus far been reported to contain only flavones (e.g., Wagner et al. 1972a; Bierner 1973, 1987; Averett and Beaman 1975; Bohm 1977). Furthermore, the compounds in *Amblyolepis* were flavonol galactosides, which have only rarely been isolated from other taxa in the subtribe (Wagner et al. 1972b, c). The occurrence of quercetin 3-*O*-galactoside and isorhamnetin 3-*O*-galactoside in both *Amblyolepis* (Bierner 1979) and *Hymenoxys* Cass. (Wagner et al. 1972c) could be dismissed as coincidental, because the same compounds have been reported from other, phylogenetically remote species, including members of the Cactaceae and Guttiferae (Harborne and Williams 1975). These chemical similarities, however, may be indicative of a true relationship between *Amblyolepis* and *Hymenoxys*, and it is notable that recent chloroplast DNA work (Kim et al. 1989, personal communication) also suggests a connection between these two genera.

Cytologically, *Amblyolepis setigera* has been reported to be  $n=19$  (Turner 1959, 1978; Raven and Kyhos 1961) and  $n=18$  (Harms 1969). Also, there are voucher specimens at LL and US (Powell and Turner 2730) indicating a count of  $n=17$  attributed to Powell; however, Powell (personal communication) could find no record of this when asked if further information might be available.

I have found populations containing plants with chromosome numbers of 18, 19, and 20 pairs plus univalents in various combinations, as presented in Table 1. In population *Bierner 88-41*, precocious division of one bivalent in plants with  $2n=20_{II}$  made some of the microsporocytes appear to be  $2n=19_{II} + 2_I$ . This also occurred in population *Bierner 88-45*, with  $2n=19_{II}$  appearing to be  $2n=18_{II} + 2_I$  in one plant. The count of  $2n=18_{II} + 3_I$  in *Bierner and Rader 51200*, therefore, may actually have been  $2n=19_{II} + 1_I$ .

The predominant chromosome number in *Amblyolepis setigera* is  $2n=18_{II}$ . The variant numbers are scattered randomly throughout a



TABLE 1. CHROMOSOME NUMBERS IN *AMBLYLEPIS SETIGERA*. Bud material was fixed in a modified Carnoy's solution: chloroform, absolute ethanol, and glacial acetic acid (4:3:1; V:V:V). The chromosomes were stained with acetocarmine, and counts were obtained from microsporocytes at diakinesis or metaphase I. All collection numbers are those of M. W. Bierner, and vouchers are deposited at TEX. Exact locality data can be found in the list of representative and cytologic voucher specimens.

| Chromosome numbers (2n)  | Vouchers   |
|--|--|
| 18 <sub>II</sub>   | MEXICO. Coahuila, 51213. USA. Texas, Coleman Co., 88-16. Jones Co., 88-10, 88-12, 88-13. Karnes Co., 88-20. Live Oak Co., 51520, 88-28. Llano Co., 88-1. McCulloch Co., 88-17. San Saba Co., 88-3, 88-5. |
| 18 <sub>II</sub> ; 18 <sub>II</sub> + 1 <sub>I</sub>   | Texas, Karnes Co., 88-24. McCulloch Co., 88-18.  |
| 18 <sub>II</sub> ; 19 <sub>II</sub>  | Texas, Val Verde Co., 88-45.   |
| 18 <sub>II</sub> + 1 <sub>I</sub> ; 18 <sub>II</sub> + 3 <sub>I</sub>  | Texas, Madina Co., 51200.  |
| 18 <sub>II</sub> ; 18 <sub>II</sub> + 1 <sub>I</sub> ; 19 <sub>II</sub> ; 19 <sub>II</sub> + 1 <sub>I</sub> ; 20 <sub>II</sub> | Texas, Webb Co., 88-41.  |

large portion of the taxon's range, and when I reexamined the specimens from these populations, I could find no correlation of morphologic characters with chromosome number. It is my opinion, therefore, that these populations are all part of a single taxon, and there is no reason to recognize more than one entity.

These chromosome numbers, except for 2n=20<sub>II</sub>, are within the range of other numbers reported for members of the Gaillardiiinae. It has been my observation, however, that the chromosomes in *Amblyolepis setigera* are ca. twice as large as those I have seen in *Gaillardia*, *Helenium*, *Hymenoxys*, and *Tetraneuris* E. Greene. Furthermore, judging from configurations of bivalents at diakinesis and metaphase, *A. setigera* appears to have more metacentric and fewer acrocentric or telocentric chromosomes than the above mentioned genera.

*Amblyolepis* is included in subtribe Gaillardiiinae and placed close to *Helenium* by most workers, mainly because of its truncated style branches and apparently naked receptacle (Correll and Johnston 1970; Robinson 1981). I find, however, that the receptacle almost always has persistent projections subtending the central disc florets, and rarely there are even a few chaffy scales subtending some of the outer disc florets. It is my overall impression from morphologic, chemical, and cytologic evidence that *Amblyolepis* is very different from the other genera in this subtribe; however, I have retained it here because of the chloroplast DNA work (Kim et al. 1989) indicating that it is in fact most closely related to taxa in the Gaillardiiinae and that its affinities may lie with *Hymenoxys*.



## TAXONOMY

*AMBLYOLEPIS* DC., Prodr. 5:667–668. 1836.—TYPE: *Amblyolepis setigera* DC.—*Helenium* L. sect. *Amblyolepis* (DC.) Benth., J. Linn. Soc. (Bot.) 13:335. 1873.

*AMBLYOLEPIS SETIGERA* DC., Prodr. 5:667–668. 1836.—TYPE: United States, Texas, “de Bejar & Austin,” [between San Antonio and Austin] 1828, J.L. Berlandier 1830 (holotype, G-DC No. 1613!).—*Helenium setigerum* (DC.) Britt. & Rusby, Trans. N.Y. Acad. Sci. 7:11. 1887.

Plants annual, 1–6 dm tall. Stems 1 to usually several, unbranched or sparingly branched above, densely long-pilose at the base becoming sparingly pilose above. Leaves entire, rarely glabrous, almost always at least sparsely to moderately long-pilose, usually more densely pubescent on the margins. Basal and lower leaves oblanceolate to spatulate, narrowed at the base; middle leaves lanceolate to ovate, usually with acute apices and semiclasping bases; upper leaves when present the same shape as middle ones but smaller, or lacking and the plant essentially naked the upper one-third to one-half. Peduncles (4)8–20 cm long, expanded apically, sparsely long-pilose below becoming moderately to densely so above. Heads 1 to usually several per plant, hemispheric to globoid at anthesis, 9–17 mm high, 12–20 mm in diameter excluding the rays; heads expanding and often becoming globose in fruit, 2–3 cm in diameter. Receptacle ovoid to globoid, 4.5–6.0 mm high, 4.5–7.5 mm in diameter; appearing at first to be naked, but almost always with persistent projections subtending the central disc florets, and rarely with a few chaffy scales subtending some of the outer disc florets. Involucral bracts in two series; the outer bracts green, usually 8, 8.8–11.2 mm long, 2.5–4.6 mm wide, narrowly elliptic to lanceolate, usually free, but sometimes united at their bases, moderately to densely long-pilose, especially at the bases and on the entire margins; the inner bracts hyaline and scale-like, usually 9–12, 3.0–4.9 mm long, 1.0–2.8 mm wide, obovate, free, glabrous, margins entire to occasionally somewhat fimbriate at the apex. Ray florets carpellate, fertile, usually 8–10, but often 12–13 or rarely as many as 20; ligules yellow, glabrous, 10–22 mm long, 4.5–9.6(11.6) mm wide. Disc florets hermaphroditic, fertile; corollas yellow, glabrous, 5-lobed, narrowly funnelform to cylindric-campanulate, usually constricted into a narrower tube the lower one-third, 5.1–7.0 mm long, 1.2–1.8 mm in diameter. Achenes narrowly obconic, 3.0–4.5 mm long, 1.7–2.2(2.6) mm in diameter, strongly 10-ribbed, densely pubescent with straight, forked, antrorse hairs. Pappus scales 5–6, ovate to obovate, apex rounded to acute, acuminate, or rarely cuspidate, but not truly awned, 2.0–3.0(4.1) mm long, 1.0–2.1 mm wide. Chromosome numbers:  $2n=17_{II}(?)$ ,  $18_{II}$ ,  $18_{II} + 1_I$ ,  $19_{II}$ ,  $18_{II} + 3_I(?)$ ,  $19_{II} + 1_I$ ,  $20_{II}$ .



*Distribution.* Northeastern Mexico in the states of Coahuila, Nuevo León, and Tamaulipas, and south Texas along the Rio Grande to the trans-Pecos and panhandle areas of Texas (Fig. 1), mostly in sandy or sandy loam soils. Flowering January to September, mainly March to May.

*Representative and cytologic voucher (\*) specimens.* MEXICO, Coahuila, hwy 57, 39.4 mi S of Allende, 21 May 1975, *Biernier and Rader 51213\** (TEX); 28 mi N of Allende, 21 May 1974, *Powell and Turner 2730\** (LL, US). Nuevo León, Mamulique Pass, 20 mi S of Sabinas Hidalgo, 16 Mar 1976, *Whalen 333\** (LL). Tamaulipas, 14 mi S of Nuevo Laredo, 24 Mar 1944, *Heard and Barkley 14596* (TEX, US).

USA, Texas, Andrews Co., ca. 11 mi SW of Andrews, 27 Apr 1961, *Correll and Rollins 23920* (LL). Brewster Co., Chisos Mts, 15 Mar 1941, *Warnock 440* (LL, TEX). Coleman Co., hwy 283 S of Santa Anna, 7.1 mi N of the Colorado River, 10 Apr 1988, *Biernier 88-16\** (TEX). Comal Co., Comanche Spring, New Braunfels, May 1850, *Lindheimer 854* (MO, NY, TEX, US). Gillespie Co., Stonewall, 17 Apr 1954, *Turner 3376\** (TEX). Hidalgo Co., 3 mi N of La Joya, 8 Jun 1941, *Runyon 2747* (TEX). Howard Co., Big Springs, 11 May 1902, *Tracy 7887* (MO, NY, TEX, US). Irion Co., 1 mi S of Mertzon, 24 Apr 1948, *Warnock 7696* (LL, TEX). Jim Hogg Co., 5 mi E of Hebbronville on hwy 285, 17 Mar 1963, *Chavez et al. 48* (LL, TEX). Jim Wells Co., 10 mi N of Premont on hwy 281, 31 Mar 1963, *Gamboa and Dohnke 142* (TEX). Jones Co., 1.8 mi E and 1.6 mi W of hwy 1226 on hwy 180 (jct in Funston), 10 Apr 1988, *Biernier 88-10\** and *88-12\** (TEX); 8.2 mi W of hwy 277 on hwy 180 (jct in Anson), 10 Apr 1988, *Biernier 88-13\** (TEX). Karnes Co., 0.3 mi W of hwy 123 on hwy 81, 14 Apr 1988, *Biernier 88-20\** (TEX); 3.9 mi SW of hwy 81 on hwy 181 (jct in Hobson), 14 Apr 1988, *Biernier 88-24\** (TEX). Kent Co., 2 mi E of Clairemont on hwy 380, 18 May 1959, *Correll and Johnston 22096* (LL). Kinney Co., 2–3 mi W of Brackettville, 30 Mar 1960, *Gentry and Barclay 18467* (LL, US). Kleberg Co., Kingsville, 11 Apr 1905, *Tracy 8956* (MO, NY, TEX, US). Live Oak Co., 5.1 mi SW of hwy 281 on hwy 59, 24 Mar 1976, *Biernier and Harborne 51520\** (TEX); 3 mi N of hwy 534 on hwy 796, 14 Apr 1988, *Biernier 88-28\** (TEX). Llano Co., 6.7 mi W of hwy 1431 on hwy 29 between Burnet and Llano, 8 Apr 1988, *Biernier 88-1\** (TEX). Lubbock Co., Shallowater, 15 Jun 1926, *Studhalter 1225* (LL). McCulloch Co., hwy 283 N of Fife, 0.2 mi and 1.5 mi S of the Colorado River, 10 Apr 1988, *Biernier 88-17\** and *88-18\** (TEX). Medina Co., S of Devine, 2.2 mi NW of hwy 472 on hwy 173, 18 May 1975, *Biernier and Rader 51200\** (TEX). Midland Co., Midland, 8 May 1902, *Tracy 7833* (MO, NY, TEX, US). Nolan Co., Sweetwater, 6 Jun 1926, *Palmer 30480a* (MO, TEX). Randall Co., Canyon, 20 May 1931, *Neelley s.n.* (TEX). Reeves



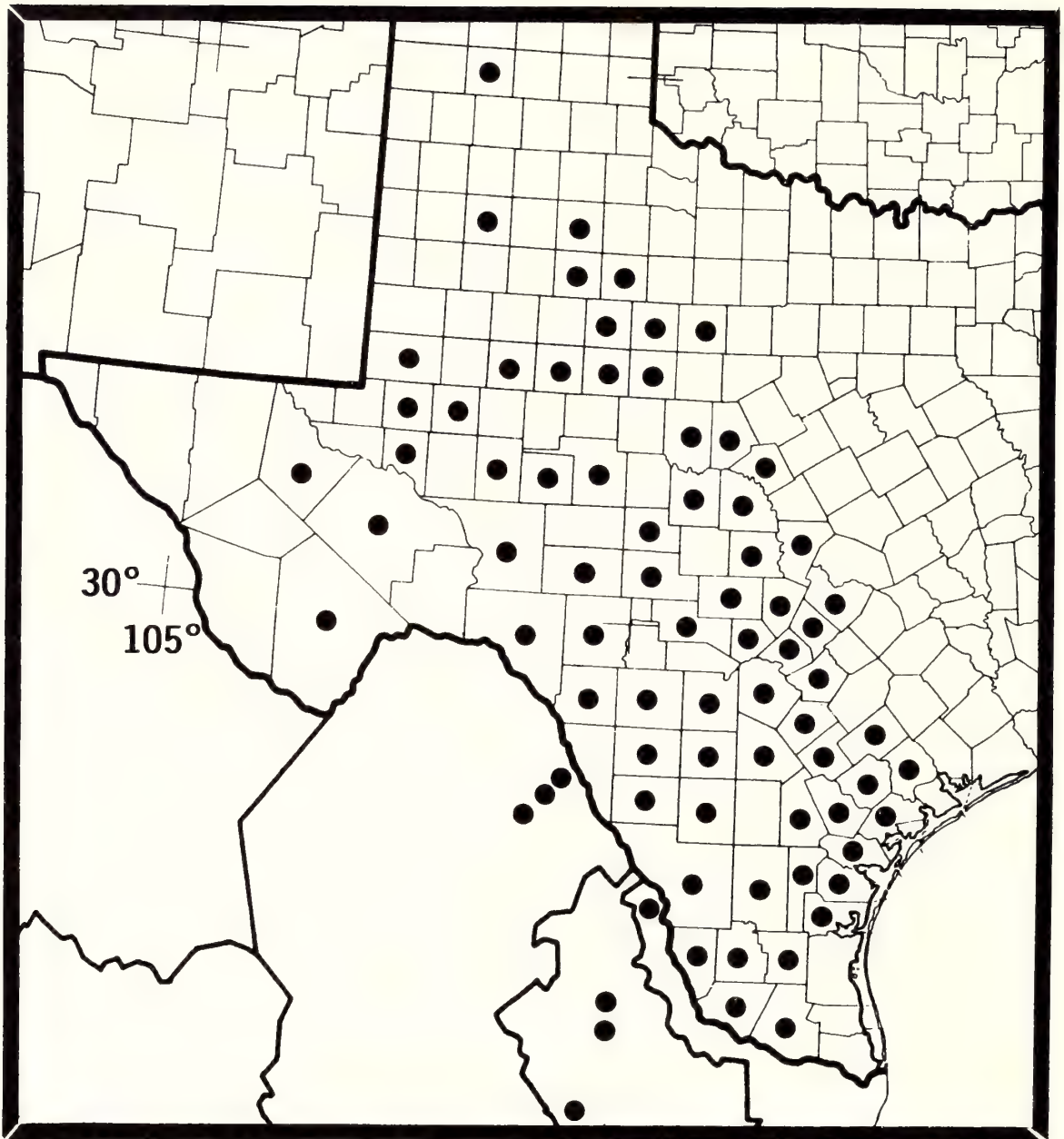


FIG. 1. Distribution of *Amblyolepis setigera*.

Co., vicinity of Pecos, 9 Jun 1931, *Gillespie* 5266 (US). Refugio Co., Refugio, 8 Mar 1916, *Palmer* 9109 (MO). San Saba Co., 1.3 mi S of hwy 190 on hwy 16 (jct in San Saba), 8 Apr 1988, *Biernier* 88-3\* (TEX); 0.3 mi S of the San Saba-Mills Co. line on hwy 16, 8 Apr 1988, *Biernier* 88-5\* (TEX), Sutton Co., Sonora, 23 May 1929, *Wright* 5 (TEX). Travis Co., Colorado River opposite Deep Eddy in Austin, 26 Apr 1936, *Tharp* 44500 (NY). Val Verde Co., 8.3 mi N of hwy 90 on hwy 163 (jct in Comstock), 16 Apr 1988, *Biernier* 88-45\* (TEX). Victoria Co., 10 mi SW of Victoria along hwy 59, 9 Apr 1964, *Gentry and Smith* 20525 (US). Webb Co., 22.6 mi NW of IH-35 on hwy 83, 15 Apr 1988, *Biernier* 88-41\* (TEX). Zavala Co., Crystal City, 14 Jun 1928, *Tharp* s.n. (TEX).



## ACKNOWLEDGMENTS

I thank the curators of the following herbaria for the loan of specimens: LL, MO, NY, TEX, and US. This work was done while I was at the University of Tennessee, Knoxville; Wild Basin Wilderness Preserve, Austin, Texas; and Southwest Texas State University, San Marcos. It was supported in part by NSF grant DEB74-17454.

## LITERATURE CITED

- AVERETT, J. E. and W. C. BEAMAN. 1975. Chemotaxonomy and flavonoids of *Gaillardia* section *Hollandia* (Asteraceae-Helenieae). *Plant Syst. Evol.* 123:237-240.
- BENTHAM, G. and J. D. HOOKER. 1873. *Genera Plantarum* 2:414. Reeve and Co., London.
- BIERNER, M. W. 1973. Chemosystematic aspects of flavonoid distribution in twenty-two taxa of *Helenium*. *Biochem. Syst. Ecol.* 1:55-57.
- . 1979. Flavonol 3-glycosides in *Amblyolepis setigera*. *Phytochemistry* 18: 358.
- . 1987. Taxonomy of *Helenium* sect. *Actinea* (Asteraceae). *Sida* 12:253-271.
- BOHM, B. A. 1977. Helenieae—chemical review. Pp. 739-768 in V. H. Heywood, J. B. Harborne, and B. L. Turner (eds.), *The biology and chemistry of the Compositae*. Academic Press, London.
- CORRELL, D. S. and M. C. JOHNSTON. 1970. P. 1674 in *Manual of the vascular plants of Texas*. Texas Research Foundation, Renner.
- DE CANDOLLE, A. P. 1836. *Prodromus systematis naturalis regni vegetabilis* 5:667-668. Treuttel and Wurtz, Paris.
- GRAY, A. 1874. Notes on Compositae and characters of certain genera and species. *Proc. Amer. Acad. Arts* 9:187-218.
- HARBORNE, J. B. and C. A. WILLIAMS. 1975. Flavone and flavonol glycosides. Pp. 376-441 in J. B. Harborne, T. J. Mabry, and H. Mabry (eds.), *The flavonoids*. Academic Press, New York.
- HARMS, L. J. 1969. Documented plant chromosome numbers 1969:3. *Sida* 3:356-357.
- HERZ, W. 1977. Sesquiterpene lactones in the Compositae. Pp. 337-357 in V. H. Heywood, J. B. Harborne, and B. L. Turner (eds.), *The biology and chemistry of the Compositae*. Academic Press, London.
- and S. V. BHAT. 1970. Coumarin in *Amblyolepis setigera*. *Phytochemistry* 9:817.
- HOFFMANN, O. 1894. Compositae in A. Engler and K. Prantl (eds.), *Die Naturl. Pflanzenfam.* 4(abt. 5):263. Verlag von Wilhelm Engelmann, Leipzig.
- KIM, K.-J., R. K. JANSEN, B. L. TURNER, T. J. MABRY, G. NESOM, and J. NORRIS. 1989. Phylogenetic implications of chloroplast DNA restriction site variation in the tribe Heliantheae (Asteraceae) [Abstract]. *Amer. J. Bot.* 76(6, Supplement): 252.
- RAVEN, P. H. and D. W. KYHOS. 1961. Chromosome numbers in Compositae. II. Helenieae. *Amer. J. Bot.* 48:842-850.
- ROBINSON, H. 1981. A revision of the tribal and subtribal limits of the Heliantheae (Asteraceae). *Smithsonian Contr. Bot.* 51:1-102.
- RYDBERG, P. A. 1915. *North American Flora* 34:131. The New York Botanical Garden, New York.
- SEAMAN, F. C. 1982. Sesquiterpene lactones as taxonomic characters in the Asteraceae. *Bot. Rev.* 48:121-595.
- SWAIN, T. and C. A. WILLIAMS. 1977. Heliantheae—chemical review. Pp. 673-698 in V. H. Heywood, J. B. Harborne, and B. L. Turner (eds.), *The biology and chemistry of the Compositae*. Academic Press, London.
- TORREY, J. and A. GRAY. 1842. *Flora of North America* 2:383. Wiley and Putnam, New York and London.



- TURNER, B. L. 1959. Meiotic chromosome counts for 12 species of Texas Compositae. *Brittonia* 11:173–176.
- . 1978. Asteraceae in A. Love (ed.), IOPB chromosome number reports. LXII. *Taxon* 27:519–535.
- YOSHIOKA, H., T. J. MABRY, and B. N. TIMMERMANN. 1973. Sesquiterpene lactones. Univ. of Tokyo Press, Tokyo.
- WAGNER, H., M. A. IYENGAR, and W. HERZ. 1972a. Flavone-C-glycosides in a coastal race of *Gaillardia pulchella*. *Phytochemistry* 11:851.
- , ———, L. HORHAMMER, and W. HERZ. 1972b. Flavonol-3-glycosides in *Plummera ambigens*. *Phytochemistry* 11:2633.
- , ———, ———, and ———. 1972c. Flavonol-3-glycosides in eight *Hymenoxys* species. *Phytochemistry* 11:3087–3088.

(Received 3 Apr 1989; revision accepted 10 Nov 1989.)

---

## NOTEWORTHY COLLECTIONS

### WYOMING

*CHLORIS VERTICILLATA* Nutt. (POACEAE).—Goshen Co.: Fort Laramie National Monument, 12 mi SE of Guernsey, in relatively undisturbed steppe near visitor's center with *Bouteloua*, *Buchlœe*, and *Setaria*, T26N R64W S20, 1310 m, 23 Sep 1989, Snow 5764 (RM).

*Significance.* First record for WY and a range extension westward of ca. 100 km from Dawes Co., Nebraska.—NEIL SNOW, Department of Botany, University of Wyoming, Laramie, WY 82071-3165.



CHROMOSOME COUNTS IN SECTION *SIMIOLUS* OF  
THE GENUS *MIMULUS* (SCROPHULARIACEAE).  
XI. *M. GLABRATUS* COMPLEX (Cont.)

ROBERT K. VICKERY, JR., FAHIMA RAHMAN,  
STEVEN R. PACK, and THONG MAC

Department of Biology, University of Utah, Salt Lake City, UT  
84112

ABSTRACT

Chromosome counts of  $n=15$  were obtained for 5 populations of *Mimulus glabratus* subsp. *fremontii* from southern Canada, central United States and northern Mexico. A count of  $n=15$  was obtained for *M. glabratus* subsp. *michiganensis*, a taxon in Category 2 on the Endangered Species list. Counts of  $n=31$  were obtained for 5 populations of *M. g.* subsp. *glabratus* from Colombia. A count of  $n=46$  was obtained for 1 population of *M. andicolus* from northern Argentina. Counts of  $n=46$  were obtained for 9 populations from the eastern slopes of the Andes and 1 population from the western slope—all belonging to *M. pilosiusculus*. The results filled in geographic gaps in the *M. glabratus* complex's north-to-south, mixoploid chromosome series of  $n=15 \rightarrow n=30 \rightarrow n=31 \rightarrow n=46$ .

RESUMEN

Recuentos de cromosomas de  $n=15$  se obtuvieron de 5 poblaciones de *Mimulus glabratus* subsp. *fremontii* del sur de Canadá, el centro de los E.E.U.U., y el norte de México. Un recuento de  $n=15$  se obtuvo de *M. glabratus* subsp. *michiganensis*, un taxón en la Categoría 2 de la lista de Especies Peligradas. Recuentos de  $n=31$  se obtuvieron de 5 poblaciones de *M. g.* subsp. *glabratus* de Colombia. Un recuento de  $n=46$  se obtuvo de una población de *M. andicolus* del norte de Argentina. Recuentos de  $n=46$  se obtuvieron de 9 poblaciones de las laderas orientales de los Andes y 1 población de la ladera occidental—todas ellas perteneciendo a *M. pilosiusculus*. Los resultados rellenan los vacíos geográficos del complejo de norte a sur en la serie mixoploide de cromosomas de  $n=15 \rightarrow n=30 \rightarrow n=31 \rightarrow n=46$ .

The *Mimulus glabratus* complex appears to have evolved by wave after wave of adaptive radiations starting from the genus' California center of diversity (Grant 1924), that is, from the probable center of origin (Vavilov 1949/50), and spreading east to Quebec and south to Patagonia (Vickery 1978). The diploids,  $n=15$ , occur inland in North America from southern Canada to central Mexico. The eutetraploids,  $n=30$ , are found in the Rio Grande drainage of Texas whereas the aneuploid tetraploids,  $n=31$ , occur from western Mexico south into Guatemala and then again in the highlands of Colombia. The hexaploids,  $n=46$ , range from Ecuador south along both sides of the Andes to the Río Santa Cruz, Argentina, that is, almost to Tierra del Fuego. There are some large gaps in our knowledge of these chromosome numbers. The purpose of this research is to im-



prove our knowledge of the distribution of chromosome numbers by improving our sampling of this widespread complex with its vast, 10,000 km north to south, Western Hemisphere range.

### MATERIALS AND METHODS

A living collection of 22 study populations was assembled in the University of Utah greenhouse. The plants were propagated from seeds collected by the senior author or his collaborators (Table 1). Chromosome counts were made from various stages of microsporangogenesis using standard aceto-carmin squash methods as previously described (Vickery et al. 1985). Twenty or more cells were studied from an average of 4 plants of each population. Representative cells were recorded with sketches or camera lucida drawings.

### RESULTS AND DISCUSSION

At the diploid level, counts of  $n=15$  were obtained for 5 widely scattered populations of *M. glabratus* subsp. *fremontii*. They ranged from southern Canada to northern Mexico. Two of the populations, culture numbers 7706 from Epoufette, Upper Peninsula, Michigan, and 10226 from near Amos, western Quebec, had been thought to belong to *M. glabratus* subsp. *michiganensis*, chiefly on geographic grounds. However, they were found to belong to the widespread, polymorphic subsp. *fremontii* instead when grown beside and compared to authentic material of subsp. *michiganensis* kindly sent to us by Margaret Bliss. *Mimulus glabratus* subsp. *michiganensis* is a Category 2 candidate for listing as endangered or threatened under the Endangered Species Act (Fish and Wildlife Service, 1985).

True *M. glabratus* subsp. *michiganensis* (Pennell 1935; Fassett 1939) has larger flowers (18–22 mm long vs. 6–12 mm long) than does subsp. *fremontii*. Also, it has longer pistils (12–20 mm vs. 5–9 mm) and ovaries (8.5–11 mm vs. 3.5–5.5 mm) than subsp. *fremontii* according to Bliss (1986). However, it has  $n=15$  chromosomes as does subsp. *fremontii* and subsp. *utahensis* (Table 1).

At the tetraploid level, 5 populations representative of the Colombian geographic race (Table 1) were found to be aneuploid tetraploids with  $n=31$  chromosomes like the Guatemalan and Mexican aneuploid tetraploid races. The Colombian aneuploid tetraploids mark the southernmost adaptive radiation of *M. glabratus* subsp. *glabratus* as well as the successful crossing of the tropics of Panama into northern South America.

At the hexaploid level, an  $n=46$  chromosome count was obtained for a population of *M. andicolus* from northern Argentina, the center of distribution of that species. Also,  $n=46$  chromosome counts were obtained for 9 populations from along the eastern slope of the Andes



TABLE 1. CHROMOSOME COUNTS IN THE *MIMULUS GLABRATUS* COMPLEX OF RELATED SPECIES AND VARIETIES. All populations, except as noted, were collected by R. K. Vickery, Jr., and grown under his culture numbers. Vouchers are in the Garrett Herbarium of the University of Utah (UT).

---

|  |
|--|
| <i>Mimulus andicolus</i> Kunth. $n = 46$ —ARGENTINA: Jujuy, Río Xibi Xibi near Jujuy, culture 11080 (Lois Arnow 3635, Oct 1971).   |
| <i>Mimulus glabratus</i> Kunth subsp. <i>fremontii</i> (Benth.) A. L. Grant. $n = 15$ —MEXICO: Chihuahua, Coyamé, culture 12186; Temosachic, culture 12191; USA: Oklahoma, Boiling Springs, culture 7132; Michigan, Epoufette, culture 7706; CANADA: Québec, d'Abitibi-Est near Amos, culture 10226 (A. Asselin et al. s.n., 1 Sep 1969).  |
| <i>Mimulus glabratus</i> subsp. <i>michiganensis</i> Pennell. $n = 15$ —USA: Michigan, Emmet Co., Maple River near Pellston, culture 13263 (Margaret Bliss s.n., Aug 1982).  |
| <i>Mimulus glabratus</i> subsp. <i>glabratus</i> . $n = 31$ —COLOMBIA: Cundinamarca, Casa Bolívar at edge of Bogotá, culture 11447; Boyaca, La Capilla near Bucaramanga, culture 13020; Tibosas near Duitama, culture 13024; edge of Sagamosa, culture 13025; Crest of Sagamosa grade, culture 13032.  |
| <i>Mimulus pilosiusculus</i> Kunth. $n = 46$ —BOLIVIA: La Paz, 3 km S of La Paz by La Paz—Oruro highway, culture 11434; at km 160 along La Paz—Oruro highway, culture 11435; by Oruro—Cochabamba highway near Caihuasi, culture 11436; beside Oruro—Cochabamba highway near Challa, culture 11437; by Oruro—Cochabamba highway, near Sayari, culture 11439; ARGENTINA: Tucuman, gap in the Tropical Forest along Tucuman—Tafi del Valle highway, culture 13034; Mendoza, Uspallata in the Mendoza Canyon, culture 13045; Mina Huemul N of Bardas Blancas, culture 13046; Río Negro, Lago Gutierrez, culture 13065; PERU: Arequipa, Hipíco-Militar at Chilina, culture 13072. |

---

from the alto plano of Bolivia to southern Argentina. In addition, the western Andes population from Arequipa, Peru was found to be a hexaploid,  $n=46$ . Previous work had suggested to us that the eastern and western Andes populations were partially separated by reproductive isolation taking the form of lower interpopulation seed sets in crosses between the two races (Vickery 1978). Due to the variability and plasticity of these plants (monkey flowers, or *mozzos* as they are called in Bolivia, or *berros* as in Argentina and Mexico), we found it difficult if not impossible to distinguish the eastern and western Andes races morphologically. Therefore, we are taking the conservative approach and are using the older name, *M. pilosiusculus* Kunth (Humboldt et al. 1817) for both races rather than a newer name such as *M. parviflorus* Lindl. or *M. glabratus* var. *parviflorus* (Lindl.) A. L. Grant for one of them as do Reiche (1911) and Grant (1924).

These additional chromosome counts revealed no surprises such as other aneuploids or octoploids. The counts filled in significant gaps, specifically in the Great Lakes area, Colombia, and the eastern Andes in the sampling of the *M. glabratus* complex. These new counts nicely corroborate the unusual, north-to-south mixoploid series of races— $n=15 \rightarrow 30 \rightarrow 31 \rightarrow 46$  (Vickery 1978; Vickery et al. 1985).



## ACKNOWLEDGMENTS

We appreciate the support of the N.I.H. Biomed Grant No. BRSG-S07-RR07092. The resumen was prepared by Raul Cano.

## LITERATURE CITED

- BLISS, M. 1986. The morphology, fertility and chromosomes of *Mimulus glabratus* var. *michiganensis* and *M. glabratus* var. *fremontii* (Scrophulariaceae). Amer. Midl. Naturalist 116:125–131.
- FASSETT, N. C. 1939. Notes from the herbarium of the University of Wisconsin—XVIII. Rhodora 41:524–529.
- FISH AND WILDLIFE SERVICE. 1985. Endangered and threatened wildlife and plants; review of plant taxa for listing as endangered or threatened species. Federal Register 50(188):39526–39584.
- GRANT, A. L. 1924. A monograph of the genus *Mimulus*. Ann. Missouri Bot. Gard. 11:99–389.
- HUMBOLDT, A. VON, A. BONPLAND, and C. S. KUNTH. 1817. Voyage de Humboldt et Bonpland. Sixieme Partie. Botanique. Nova genera et species plantarum. 2: 369–371. Libraire Grecque-Latine-Allemande, Paris.
- PENNELL, F. W. 1935. The Scrophulariaceae of eastern temperate North America. Mongr. Acad. Nat. Sci. Philadelphia 1:1–650.
- REICHE, J. S. 1911. Flora de Chile, Vol. 6, Part 1. Moneda, Barcelona.
- VAVILOV, N. I. 1949/50. The origin, variation, immunity and breeding of cultivated plants. (trans. by K. S. Chester). Chron. Bot. 13:(1/6).
- VICKERY, R. K., JR. 1978. Case studies in the evolution of species complexes in *Mimulus*. Evol. Biol. 11:404–506. Plenum, New York.
- , S. A. WERNER, D. R. PHILLIPS, and S. R. PACK. 1985. Chromosome counts in section *Simiolus* of the genus *Mimulus* (Scrophulariaceae). X. The *M. glabratus* complex. Madroño 32:91–94.

(Received 26 Sep 1989; revision accepted 8 Dec 1989.)

---

 NOTEWORTHY COLLECTIONS

## WASHINGTON

*HERIBAUDIELLA FLUVIATILIS* (Areschoug) Svedelius (PHAEOPHYTA, ECTOCARPALES, LITHODERMATACEAE). Chelan Co., between mileposts 184 and 185 on Hwy 97 (47°22'N, 120°38'W) in Peshastin Creek, 12 Aug 1989, abundant as discoid to irregular crusts, 100–150  $\mu$ m thick and 0.5–30 cm diam. on large rocks in fast flowing water (13°C) that was partially shaded, *West s.n.* (UC).

*Significance.* Brown algae are relatively rare in freshwater habitats. *Heribaudiella fluviatilis* was known previously in Europe, China, Japan, British Columbia, and one locality at Nighthawk, Washington on the Similkameen River, 200 km N of the Peshastin Creek site (Wehr and Stein. J. Phycol. 21:81–92, 1985).—JOHN A. WEST, Department of Plant Biology, University of California, Berkeley, CA 94720.



## NOTES

*BRAYA GLABELLA* VAR. *GLABELLA* (BRASSICACEAE) IN COLORADO.—*Braya glabella* Richardson var. *glabella* has been located in portions of the Sawatch Range and Elk Mountains. The first recognized collection for Colorado and the contiguous United States is: Colorado, Chaffee Co., Sawatch Range, Mineral Basin, approximately 30 km WSW of Buena Vista, 3685 m, 38°36'06"N, 106°23'45"W, 31 Jul 1987, *Siems 1592*. Additional collections include: Colorado, Chaffee Co., Sawatch Range, N-facing ridge, SE of Spout Lake, 4.8 km S of Cottonwood Pass, E of Continental Divide, 38°47'N, 107°24'29"W, 3750 m, 17 Aug 1985, *Neely 3170* (CS, RM; verified by J. Harris); Gunnison Co., Elk Mts., 0.5 km NW of American Flag Mountain, 1.4 km E of Stewart Mine, 38°56'10"N, 106°43'16"W, 3810 m, 24 Jul 1985, *Neely 3183* (CS, RM; verified by J. Harris); Elk Mts., ca. 0.8 km SE of Crystal Lake, Fossil Ridge, just NE of unnamed peak of 12,004 ft elev. (3659 m), 38°39'30"N, 106°37'41"W; 3658 m, 15 Aug 1985, *Neely 3174* (CS, RM; verified by J. Harris); Pitkin/Gunnison Co. line, Elk Mts., ridge S of Taylor Pass, 3870 m, 30 Jul 1984, *Mitchell 1698* (COLO); Elk Mts., ridge S of Taylor Pass, 3880 m, 10 Aug 1983, *Mitchell 1556* (COLO); Chaffee Co., Sawatch Range, Mineral Basin, approximately 30 km WSW of Buena Vista, 3685 m, 38°36'06"N, 106°23'45"W, 5 Aug 1988, *Weber et al. 17980* (COLO).

The most closely related species in Colorado is *Braya humilis* (C. Meyer) Robinson var. *humilis*. *Braya glabella* var. *glabella* differs from *B. humilis* in having scapose stems, with at most a single leaf or leafy bract subtending the lowermost flower or fruit, whereas *B. humilis* has leafy stems. The siliques are 3.5–8.3 times longer than broad in *B. glabella* var. *glabella* and 10–25 times in *B. humilis*. Fruits of the latter are linear, torulose, 9–29 mm long, and 0.6–1.2 mm wide. The siliques of *B. glabella* are oblong to narrowly oblong-lanceolate, occasionally torulose, 5–12 (–15) mm long, and 1.1–3 mm wide. Seeds are biseriate in *B. glabella* and uniseriate in *B. humilis*. (J. G. Harris, unpub. Ph.D. thesis, Univ. of Alberta, 1985).

In Mineral Basin, both *Braya* species occur in small patches of one to a few individuals separated by bare ground. Nearby species include *Erigeron leiomerus*, *E. compositus*, and *Antennaria aromatica*. In the adjacent Spout Lake Basin, *B. glabella* occurs alone, on loose rocks with sparse vegetative cover, associated with *Dryas octopetala*, *Carex rupestris*, *Oxytropis deflexa*, *Kobresia myosuroides*, and *Castilleja occidentalis*. Associates in the Crystal Lake and American Flag Mountain populations are similar, with additional species such as *Minuartia obtusiloba*, *Smelowskia calycina*, and *Physaria alpina*.

*Braya glabella* var. *glabella* is a North American lower arctic, sub-arctic, montane and alpine taxon, with most of its reported occurrences north of 60° latitude. It occurs in Alaska and in Alberta, British Columbia, Northwest Territories, Yukon, and Quebec in Canada. The distribution ranges south from the Canadian Arctic Archipelago through the Mackenzie and Rocky Mountains to Athabasca Glacier and Cardinal River, Alberta, west to Seward Peninsula, Alaska, and east to Hudson Bay (Harris 1985). The most northerly occurrence is on Banks Island in Northwest Territories (at approximately 74°N). Its distribution is somewhat similar to the North American distribution of *B. humilis*. However, *B. glabella* var. *glabella* is reported from fewer locations, does not extend as far north, and is apparently absent on the southwest side of Hudson Bay, where *B. humilis* is not infrequent. Throughout its North American range, *Braya humilis* is believed to be exclusively or nearly exclusively associated with calcareous substrates. In Canada, *Braya glabella* often occurs on calcareous barren soils and gravels on gravel bars, disturbed sites, lake and seashores, scree slopes, and solifluction lobes (Harris 1985).



The closest previous *Braya glabella* var. *glabella* record is from an estimated 53°N latitude in Jasper National Park, Canada (Harris 1985), approximately 1800 km north of the Colorado populations. The Colorado collections represent a greater distance of disjunction than do the Colorado *B. humilis* populations (disjunct from populations in Waterton Lakes Park, Alberta).

In the Colorado alpine only five small populations of *Braya glabella* are known, and these are spread through three counties and two mountain ranges (the Elk Mountains and the Sawatch Range). *Braya humilis* var. *humilis* is known from about 20 populations in 10 locations in four mountain ranges in Colorado (the Tenmile, Mosquito, Sawatch, and Elk ranges).

The two species appear to be ecologically very similar. In Colorado *Braya humilis* var. *humilis* is restricted to calcareous soils associated with the Paleozoic Leadville Limestone and Manitou Dolomite (Neely and Carpenter, Great Basin Naturalist 46: 728–735, 1986). Typical habitats include solifluction lobes, low angle talus slopes, and gravel associated with minor amounts of soil movement, as well as man-made disturbances, usually mining associated. In Mineral Basin, *B. glabella* var. *glabella* occurs with *B. humilis* in highly calcareous, disturbed, inorganic mineral soil. The populations occur below a 320-meter thick section of Paleozoic limestones and dolomites which form cliffs and moderately steep to steep, stable and unstable talus slopes. Although the sampled population occurs in association with material disturbed by mining activities within the last century, source populations probably occur on the naturally disturbed area upslope. One collection (Mitchell 1698) is described as being from granite talus, but the same Paleozoic carbonate formations are known to occur in the area and may have contributed to the soil. With that one doubtful exception, *B. glabella* var. *glabella* in Colorado is always found on calcareous substrates derived from Mississippian Leadville Limestone, with or without materials derived from other Paleozoic calcareous formations. It occurs at or above 3658 m, on sparsely vegetated slopes above timberline, with fine gravels, or on disturbed sites associated with inactive mines.

The area encompassing Mineral Basin and Spout Lake is potentially comparable to Horseshoe Basin, noted by Weber and Argus (Madroño 33:148–9, 1986) as being “part of the most critical floristic site in the state” because of its extensive exposures of alpine limestone. Such limestone outcrops characterize this area also. Available habitats include broad expanses of calcareous talus, stabilized talus/fan deposits, exposed ridgetops, two lake shores, perennially wet turf, and springs. Both north- and south-facing basins occur. Especially notable is the expanse of south-facing cliffs, unstable talus, and frost-disturbed slopes. Much of this area would have been above any glaciers filling the cirque basin. The steepness and south-facing aspect make a potentially ideal refuge for disturbance-adapted calciphilous species during Pleistocene full-glacial times. Harris (1985) suggests that such unglaciated areas were of primary importance in the survival of *Braya* species in many areas of northern North America because these species lack long distance dispersal mechanisms and are almost entirely restricted to calcareous soils. Several new carbonate associated species have been reported in Colorado in recent years, including *Antennaria aromatica*, *Chondrophylla nutans*, *Salix lanata* subsp. *calcicola*, and now, *B. glabella* var. *glabella*. It is possible that other disjunct species occur within the estimated 2 km<sup>2</sup> area of Paleozoic carbonate units where Mineral Basin and Spout Lake are located.

We thank Emily Hartman and Mary Lou Rottman, Univ. Colo., Denver, for sharing their love of the tundra and especially Mineral Basin. We also thank J. Harris for his prompt verification of selected samples and for allowing material from his thesis to be included in this manuscript. The support and encouragement of Wm. A. Weber, (Univ. Colo., Boulder), J. L. Proffitt (WIDCO, Centralia, WA), and A. Carpenter (The Nature Conservancy, Boulder, CO) have been deeply appreciated. —BARBARA A. SIEMS, Botany Department, Univ. of Washington, Seattle, WA 98195 and ELIZABETH E. NEELY, Colorado Field Office, The Nature Conservancy, 1244 Pine St., Boulder, CO 80302. (Received 9 May 1989; revision accepted 17 Dec 1989.)



## REVIEW

*Rare Plants of Colorado*. By THE COLORADO NATIVE PLANT SOCIETY. 1989. Rocky Mountain Nature Association, Rocky Mt. National Park, Estes Park, CO 80517. 75 pages; color photographs and illustrations: softcover \$7.95 + \$2.50 shipping & handling; Colorado residents add 3% sales tax.

Conservation organizations continually need summarized information about rare species to interest the general public, inform the novice botanist as well as the professional, and focus environmental awareness on the fragility of familiar landscapes. *Rare Plants of Colorado* meets these public information needs with elegance and style in a beautifully illustrated magazine format.

The editors' stated goals were to collect the most complete information available about almost 100 of the rarest species in Colorado, and to publish this information in a concise illustrated form that would increase general awareness and understanding of these plants and their habitats. This, they hoped, would stimulate further study of Colorado's rare plants and the habitats that appear particularly vulnerable to loss or damage.

Ninety-three species of plants are grouped into 8 habitat classifications including tundra, barrens, cliffs and canyons, forests, grasslands, shrublands, wetlands, and woodlands. This type of organization may be, at first, irritating to a botanist's taxonomic instincts, but provides an ideal way to discuss the fragility of the landscape. Each of these habitats is discussed in terms of conditions to which the plant life must be adapted, special communities which are found in the larger habitat, and particular threats to the habitat. This format allows the writers to present more ecological information to the general public than a phylogenetic arrangement could.

An illustration and a general location map for each species are accompanied by details of general interest, such as reasons for rareness, botanical history associated with the plant's discovery, or the meaning of the specific epithet. A wealth of information is packed into the discussion of each species for those willing to read carefully. The rest of us can be content to enjoy the beautiful photographs and illustrations.

The book should have been edited more carefully. Errors have crept in to a few of the plant discussions, and the list of suggested readings is quite perplexing in its organization. The authors fail to mention that Colorado has many more rare plants than are presented; this fact should have been spelled out. A second omission of note is that the status of each species is, astonishingly, not one of the items addressed in the discussions. These omissions would be easily corrected with a current comprehensive list of plants of special concern and their status. Finally, while the foreword section directs the reader to become a conservation activist, it fails to tell the reader what to do or, most importantly, what not to do if they think they have found an endangered plant.

This publication does what it was designed to do: interest and stimulate. Although this is not and was not meant to be a comprehensive reference, it does compile information that has not previously been available in a single volume. I have had the opportunity to share this book with several professional conservationists. Their enthusiastic response to *Rare Plants of Colorado* indicates an unfulfilled need for current comprehensive reference materials. *Rare Plants of Colorado* is a step in the right direction.—PATRICIA BARLOW, Department of Biology, University of New Mexico, Albuquerque, NM 87131.



## ANNOUNCEMENT

## NEW PUBLICATIONS

- BOLSINGER, CHARLES L. Shrubs of California's chaparral, timberland, and woodland: Area, ownership, and stand characteristics. *U.S.D.A. Pacific Northwest Research Station, Resource Bulletin* PNW-RB-160: [i-iii], 1-50, Jan 1989, no ISSN, gratis (from PNRS, 319 S.W. Pine St., P.O. Box 3890, Portland, Oregon 97208). [With 12 tables. For companion work on hardwoods see *Taxon* 38:621.]
- CODY, WILLIAM J. and DONALD M. BRITTON. Ferns and fern allies of Canada. *Research Branch, Agriculture Canada* 1829/E: i-iv. 1-430, 1989, ISBN 0-660-12102-1, Can\$38.50 Canada, US\$46.20 foreign (from Canadian Govt. Publishing Centre, Supply and Services Canada, Ottawa K1A 0S9). [Contents: intro.; addendum to intro.; generic key; flora; maps; glossary; biblio.; index. Also in French as "Les fougères et les plantes alliées du Canada," Ibid. publ. 1829/F, ISBN 0-660-92527-3, same prices.] [On 15 fam., 35 gen., 133 spp., plus infraspecific taxa of pteridophytes (159 distribution maps), many occurring also in western U.S.]
- HUTCHINSON, JUDY L. and G. LEDYARD STEBBINS. *A flora of the Wright's Lake area: Vascular plants growing within one mile (1.5 kilometers) of Wright's Lake*. Judy L. Hutchinson, P.O. Box 142, Pollock Pines, California 95726, 1986, [v], 237 pp., illus., no ISBN, paperbound, price unknown. Handy florule for 199 spp. (9 pteridophytes, 5 conifers, 186 angiosperms) for ca. 2100 m elev. area SW Lake Tahoe.]
- MARTIN, WILLIAM C. and CHARLES R. HUTCHINS. *Fall wildflowers of New Mexico*. University of New Mexico Press, Albuquerque, New Mexico 87131, 1988, [v], 294 pp., 16 pls. (color), text illus. (B&W), ISBN 0-8263-1080-X (hardbound), \$24.95, ISBN 0-8263-1081-8 (paperbound), \$12.95. [= *New Mexico Natural History Series*, unnum. Contents: intro.; glossary; keys (to common names of fam./gen., Legum. gen., Comp. gen.); descriptions (text on versos, illus. by Robert DeWitt Ivey on facing rectos); index. Also vols. on spring (1984, [v], 257 pp.) and summer (1986, v, 318 pp.), both with 16 color pls., same price structure (see *Taxon* 36:314). This series will treat over a third of the ca. 4000 wild plants of New Mexico.]
- PIELOU, E. C. *The world of northern evergreens*. Comstock Publishing Associates, Cornell University Press, 124 Roberts Place, Ithaca, New York 14850, 1988, x, 174 pp., illus., ISBN 0-8014-2116-0 (hardbound), \$36.50, ISBN 0-8014-9429-9 (paperbound), \$10.95. [Contents: origins of evergreen forests; ten conifer groups; the species; reproduction; life and growth; insect pests; fungi and other parasites; fire, wind, snow, and air pollution; mammals and birds of coniferous forests; hardwood associates; epilog; biblio.; index.]



## SUBSCRIPTIONS—MEMBERSHIP

Membership in the California Botanical Society is open to individuals (\$22 per year; students \$12 per year for a maximum of seven years). Members of the Society receive MADROÑO free. Family memberships (\$25) include one five-page publishing allotment and one journal. Emeritus rates are available from the Corresponding Secretary. Institutional subscriptions to MADROÑO are available (\$30). Membership is based on a calendar year only. Applications for membership (including dues), orders for subscriptions, and renewal payments should be sent to the Treasurer. Requests and rates for back issues, changes of address, and undelivered copies of MADROÑO should be sent to the Corresponding Secretary.

## INFORMATION FOR CONTRIBUTORS

Manuscripts submitted for publication in MADROÑO should be sent to the editor. All authors must be members, and membership is prerequisite for review.

Manuscripts may be submitted in English or Spanish. English-language manuscripts dealing with taxa or topics of Latin America and Spanish-language manuscripts must have a Spanish RESUMEN and an English ABSTRACT.

Manuscripts and review copies of illustrations must be submitted in triplicate for all articles and short items (NOTES, NOTEWORTHY COLLECTIONS, POINTS OF VIEW, etc.). Follow the format used in recent issues for the type of item submitted. Allow ample margins all around. Manuscripts MUST BE DOUBLE SPACED THROUGHOUT. For articles this includes title (all caps, centered), author names (all caps, centered), addresses (caps and lower case, centered), abstract and resumen, text, acknowledgments, literature cited, tables (caption on same page), and figure captions (grouped as consecutive paragraphs on one page). Order parts in the sequence listed, ending with figures. Each page should have a running header that includes the name(s) of the author(s), a shortened title, and the page number. Do not use a separate cover page or "erasable" paper. Avoid footnotes except to indicate address changes. Table and figure captions should contain all information relevant to information presented. All measurements and elevations should be in metric units. Specimen citations may include English or metric distance measurements.

Line copy illustrations should be clean and legible, proportioned (including captions) to the MADROÑO page, and designed for reduction to  $\frac{2}{3}$  original size. Scales should be included in figures, as should explanation of symbols, including graph coordinates. Symbols smaller than 1 mm after reduction are not acceptable. Maps must include latitude and longitude references. Halftone copy should be designed for reproduction at actual size. In no case should original illustrations be sent prior to the acceptance of a manuscript. When needed they should be mounted on stiff cardboard and sent flat. No illustrations larger than  $22 \times 28$  cm will be accepted.

Presentation of nomenclatural matter (accepted names, synonyms, typification) should follow the format used for members of the *Allium sanbornii* complex in MADROÑO 36:124–128. 1989. Institutional abbreviations in specimen citations should follow Holmgren, Keuken, and Schofield, *Index Herbariorum*, 7th ed. Names of authors of scientific names should be abbreviated according to the Kew *Draft Index of Author Abbreviations* (1980). Abbreviation of serial titles should be those in *Botanico-Periodicum-Huntianum* (Lawrence et al., 1968, Hunt Botanical Library, Pittsburgh). If the correct abbreviation cannot be determined, the full serial title should be used. Titles of books should be given in full, together with the place and date of publication, publisher, and edition, if other than the first.

All members of the California Botanical Society are allotted five free pages per volume in MADROÑO. Joint authors may split the full page number. Beyond that number of pages a required editorial fee of \$65.00 per page will be assessed. The purpose of this fee is not to pay directly for the costs of publishing any particular paper, but rather to allow the Society to continue publishing MADROÑO on a reasonable schedule, with equity among all members for access to its pages. Printer's fees for illustrations and typographically difficult material @ \$35.00 per page (if their sum exceeds 30 percent of the paper) and for author's changes after typesetting @ \$4.50 per line will be charged to authors.

At the time of submission, authors must provide information describing the extent to which data in the manuscript have been used in other papers that are published, in press, submitted, or soon to be submitted elsewhere.





CALIFORNIA BOTANICAL SOCIETY



3  
F.

# MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

## Contents

|   |                    |
|---|--------------------|
| TAXONOMIC REVISION OF <i>VIGUIERA</i> SUBG. <i>BAHIOPSIS</i> (ASTERACEAE: HELIANTHÉAE)<br><i>Edward E. Schilling</i>  | 149                |
| A SYSTEMATIC STUDY OF <i>ANTENNARIA MEDIA</i> , <i>A. PULCHELLA</i> , AND <i>A. SCABRA</i><br>(ASTERACEAE: INULEAE) OF THE SIERRA NEVADA AND WHITE MOUNTAINS<br><i>Randall J. Bayer</i> | 171                |
| A NEW SPECIES OF <i>ERIGERON</i> (ASTERACEAE: ASTEREAE) FROM COLORADO<br><i>Steve L. O'Kane, Jr.</i>  | 184                |
| <i>POTENTILLA CRISTAE</i> (ROSACEAE), A NEW SPECIES FROM NORTHWESTERN CALIFORNIA<br><i>William J. Ferlatte and John L. Strother</i>   | 190                |
| A NEW VARIETY OF <i>PENSTEMON FREMONTII</i> (SCROPHULARIACEAE) FROM COLORADO<br><i>Robert D. Dorn and Robert W. Lichvar</i>   | 195                |
| MARITIME STRESS TOLERANCE STUDIES OF CALIFORNIA DUNE PERENNIALS<br><i>Brian H. Fink and Joy B. Zedler</i>   | 200                |
| NOTES   |                    |
| ADDITIONS TO THE VASCULAR FLORA OF YELLOWSTONE NATIONAL PARK, WYOMING<br><i>Neil Snow, B. E. Nelson, and Ronald L. Hartman</i>  | 214                |
| NOTEWORTHY COLLECTIONS  |                    |
| ARIZONA   | 216                |
| MEXICO  | 217                |
| REVIEWS   | 219                |
| MEMORIAL  | 221                |
| ANNOUNCEMENTS   | 170, 194, 218, 224 |



MADROÑO (ISSN 0024-9637) is published quarterly by the California Botanical Society, Inc., and is issued from the office of the Society, Herbarium, Life Sciences Building, University of California, Berkeley, CA 94720. Subscription rate: \$30 per calendar year. Subscription information on inside back cover. Established 1916. Second-class postage paid at Berkeley, CA, and additional mailing offices. Return requested. POSTMASTER: Send address changes to Mona Bourell, Botany Dept., California Academy of Sciences, San Francisco, CA 94118.

*Editor*—DAVID J. KEIL  
Biological Sciences Department  
California Polytechnic State University  
San Luis Obispo, CA 93407

*Board of Editors*

Class of:

- 1990—STEVEN TIMBROOK, Ganna Walska Lotusland Foundation, Montecito, CA  
THOMAS R. VAN DEVENDER, Arizona-Sonora Desert Museum, Tucson, AZ  
1991—JAMES HENRICKSON, California State University, Los Angeles, CA  
WAYNE R. FERREN, JR., University of California, Santa Barbara, CA  
1992—BRUCE A. STEIN, The Nature Conservancy, Washington, D.C.  
WILLIAM L. HALVORSON, Channel Islands National Park, Ventura, CA  
1993—JON E. KEELEY, Occidental College, Los Angeles, CA  
RHONDA L. RIGGINS, California Polytechnic State University, San Luis  
Obispo, CA

---

CALIFORNIA BOTANICAL SOCIETY, INC.

OFFICERS FOR 1990-91

- President:* THOMAS DUNCAN, University Herbarium, University of California, Berkeley, CA 94720  
*First Vice President:* MARY ANN T. SHOWERS, California Department of Parks and Recreation, Sacramento, CA 94296  
*Second Vice President:* LOREN RIESEBERG, Rancho Santa Ana Botanic Garden, Claremont, CA 91711  
*Recording Secretary:* NIALL MCCARTEN, Department of Integrative Biology, University of California, Berkeley, CA 94720  
*Corresponding Secretary:* BARBARA ERTTER, University Herbarium, University of California, Berkeley, CA 94720  
*Treasurer:* MONA BOURELL, Department of Botany, California Academy of Science, San Francisco, CA 94118  
*Financial Officer:* BARRETT ANDERSON, EIP California, San Francisco, CA 94107

The Council of the California Botanical Society consists of the officers listed above plus the immediate *Past President*, ROBERT W. PATTERSON, Biological Sciences Department, San Francisco State University, San Francisco, CA 94132; the *Editor* of MADROÑO; three elected *Council Members*: STEPHEN W. EDWARDS, East Bay Regional Park District, Regional Parks Botanic Garden, Tilden Regional Park, Berkeley, CA 94708; ELIZABETH MCCLINTOCK, University Herbarium, University of California, Berkeley, CA 94720; BARBARA PITSCHEL, Strybing Arboretum, Golden Gate Park, San Francisco, CA 94118; and a *Graduate Student Representative*, JAMES D. MOREFIELD, Rancho Santa Ana Botanic Garden, Claremont, CA 91711.

|   |
|---|
| THIS PUBLICATION IS PRINTED ON ACID-FREE PAPER. |
|---|



# TAXONOMIC REVISION OF *VIGUIERA* SUBG. *BAHIOPSIS* (ASTERACEAE: HELIANTHEAE)

EDWARD E. SCHILLING

Department of Botany, University of Tennessee,  
Knoxville, TN 37996-1100, USA

## ABSTRACT

*Viguiera* Kunth subg. **Bahiopsis** (Kellogg) stat. nov. includes twelve taxa of shrubby perennials from the Sonoran Desert of the Baja California Peninsula and nearby xeric areas that were previously included as part of *V. ser. Viguiera* (*V. ser. Dentatae* S. F. Blake). The subgenus is characterized by apomorphies involving chromosome, chemical, and molecular data but is not diagnosed by any single morphological trait, although members exhibit a distinctive combination of traits, including woody habit, phyllaries that have an indurated base and an abruptly narrowed, herbaceous apex, and leaves with subsessile glandular trichomes. The diploid species of the subgenus are well differentiated from one another, particularly by vegetative features, but the polyploid taxa are less well distinguished from each other and from related diploids, making some identifications problematical. The diploid species exhibit a series of parapatric geographic distributions, with the polyploid ones overlapping one or more diploids. A key to species of the subgenus, including the novelty here described, *V. carterae*, is presented and comments on typification of several species are included.

## RESUMEN

Se incluye en *Viguiera* Kunth subg. **Bahiopsis** (Kellogg) stat. nov. doce táxones de arbustos perennes nativos del desierto de Sonora de Baja California y áreas áridas adyacentes, los cuales originalmente estaban incluidos en la ser. *Viguiera* (ser. *Dentatae* S. F. Blake). Se ha demostrado que el subgénero está caracterizado por apomorfias tales como el número cromosómico y características químicas y moleculares, más no por ningún carácter morfológico en particular, aunque los miembros exhiben una combinación de caracteres distintiva que incluyen un hábito leñoso, filarias con una base indurada y un ápice herbáceo angosto, y por tricomas semisésiles glandulares. Las especies diploides del subgénero están bien diferenciadas unas de otras, particularmente por rasgos vegetativos, más los táxones poliploides son difíciles de distinguir entre ellos mismos y de diploides afines. Las especies diploides exhiben una serie de distribuciones geográficas parapátricas, con las especies poliploides superponiéndose a una o varias de éstas. Se provee una clave para el subgénero, la cual incluye la nueva especie *V. carterae*, al igual que comentarios sobre la tipificación de las especies incluidas.

*Viguiera* Kunth, which includes over 150 New World species, is represented in the Sonoran Desert and nearby xeric areas primarily by taxa placed previously in *Viguiera* ser. *Viguiera* (*V. ser. Dentatae* S. F. Blake). Recent analyses of chromosome numbers (Schilling and Schilling 1986), floral flavonoids (Rieseberg and Schilling 1985), and foliar flavonoid aglycones (Schilling 1989) have made it clear that *V. ser. Viguiera* is a mixed taxonomic grouping. These studies in-



dicates that the exclusion of the two species from mainland Mexico, including the nomenclatural type of *V.* ser. *Viguiera*, leaves an apparently monophyletic group of taxa from the Sonoran Desert area, for which the name subg. *Bahiopsis* (Kellogg) E. Schill. is here proposed.

*Viguiera* subg. *Bahiopsis* is distinguished by several synapomorphies involving chromosomal, chemical, and molecular features. The base chromosome number of the subgenus is  $x=18$ , which is distinctive within *Viguiera* (Schilling and Schilling 1986); most other members of the genus have  $x=17$ . The floral flavonoid complement of the subgenus includes glycosides of quercetin 3-methylether, another trait that is distinctive within *Viguiera* (Rieseberg and Schilling 1985). All species of the subgenus exhibit external flavonoid aglycones that are sequestered in subsessile glandular trichomes; although the chemistry of these compounds is fairly diverse, the subgenus appears to be characterized within *Viguiera* by the presence of 6-hydroxy,7-methoxyflavones that occur in many of the taxa (Schilling 1989). The six species of the subgenus that were included in an analysis of chloroplast DNA form a monophyletic group distinguished by seven restriction site differences compared to a diversity of other species of *Viguiera* and related genera (Schilling and Jansen 1989).

In contrast to chromosomal and chemical data, there is no single morphological trait that is diagnostic within *Viguiera* for subg. *Bahiopsis*, but its taxa exhibit a distinctive combination of traits that is found in all members of the subgenus but not in combination anywhere else in the genus. The single most characteristic feature is the nature of the phyllaries, which have an ovate, indurated base and an abruptly narrowed herbaceous apex, and this was used by Blake (1918) to delimit his *V.* ser. *Dentatae*. Such phyllaries are also exhibited by *V. dentata* (Cav.) Sprengel and *V. pinnatilobata* S. F. Blake. Other characteristic features of the subgenus include shrubby habit, monotelic thyrsoïd capitulescences with alternate arrangement of paracladia, leaves with subsessile glandular trichomes, pappus of two narrow awns and an intermediate scale on each side between the awns, and style branches that are acute and exappendiculate. In addition, the geographical distribution of the group is relatively compact, with all species inhabiting the Baja California Peninsula and nearby xeric areas (Figs. 1, 2). The only other member of *Viguiera* that is present within this area is the clearly distinctive species, *V. purisimae* Brandegees of *V.* sect. *Leighia* S. F. Blake.

The proper level at which to recognize *V.* subg. *Bahiopsis* is not completely clear, because of potential problems originating from the fact that *Viguiera*, as well as a number of its currently recognized infrageneric taxa, may be paraphyletic. Data from restriction fragment analysis of chloroplast DNA (Schilling and Jansen 1989) sug-



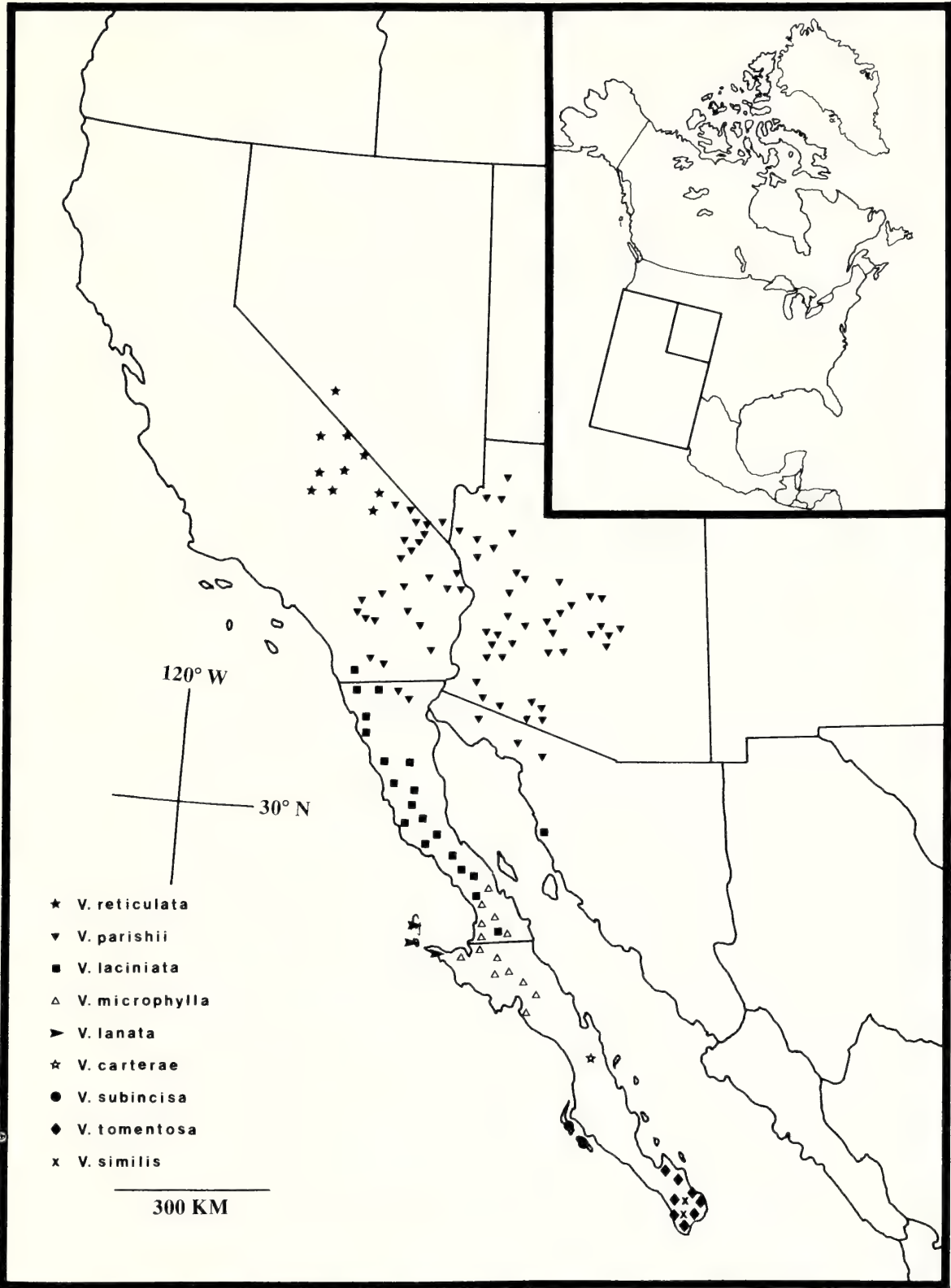


FIG. 1. Map of northwestern Mexico and the southwestern United States showing geographical distributions of the diploid species of *Viguiera* subg. *Bahiopsis*.

gest that to circumscribe monophyletic lineages while retaining related, distinctive genera (such as *Helianthus* L., *Heliomeris* Nutt., *Pappobolus* S. F. Blake [= *Helianthopsis* H. Robinson], *Simsia* Persoon, and *Tithonia* Desf. ex Jussieu), *Viguiera* may have to be split into a number of smaller genera. These data also suggest that *V.*



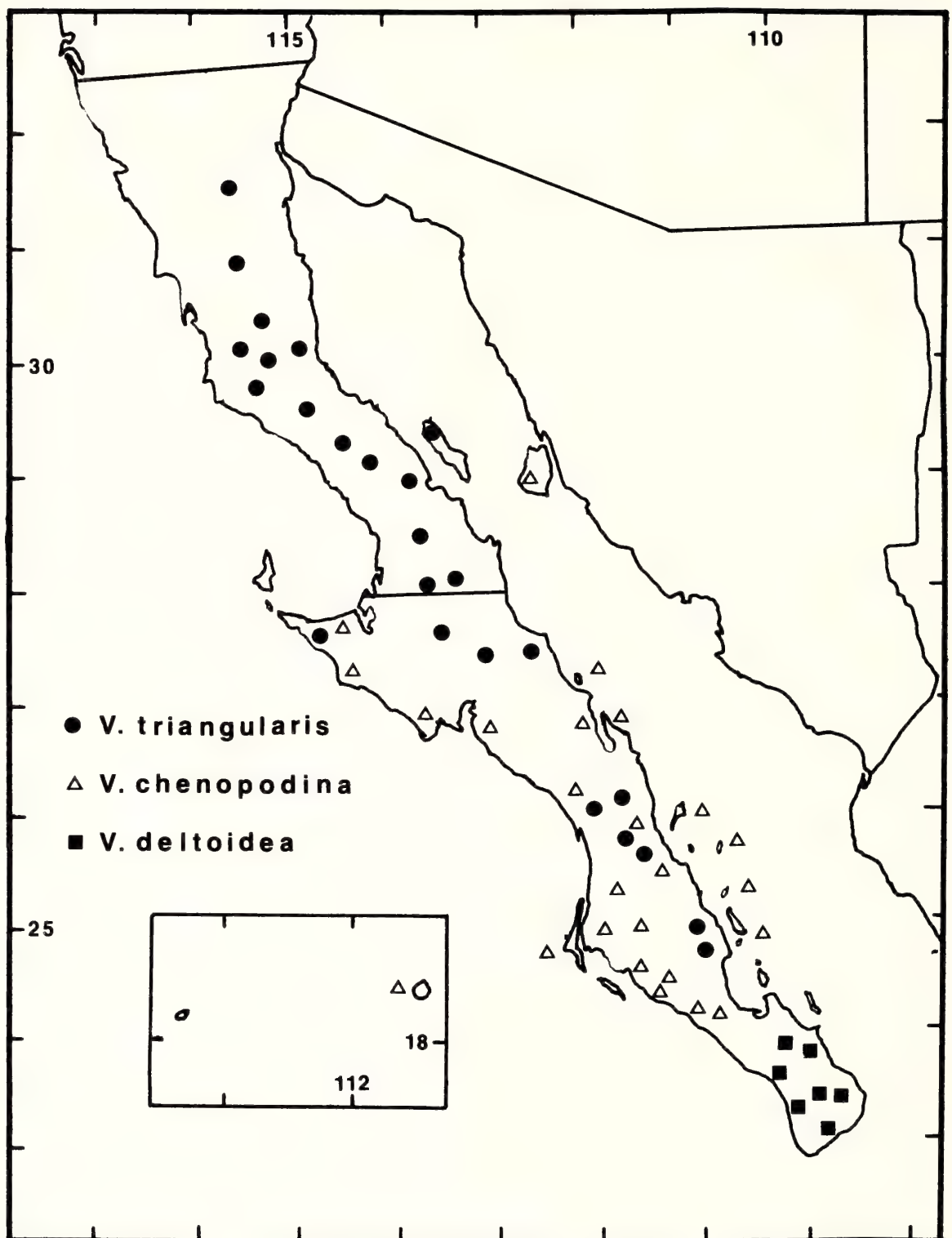


FIG. 2. Map of northwestern Mexico and the Revillagigedo Islands (inset) showing geographical distributions of the polyloid species of *Viguiera* subg. *Bahiopsis*.

subg. *Bahiopsis* may be a sister group to other members of *Viguiera* and also to related genera. A nomenclaturally conservative course is taken here, employing the name under which one of the member species (*V. lanata*) was originally described. My purpose here is to provide *V. subg. Bahiopsis* with formal recognition and to present a treatment of the taxonomy of its species.



## RELATED INFRAGENERIC TAXA

Species of *Viguiera* that are morphologically most similar to members of *V.* subg. *Bahiopsis* occur in *V.* sect. *Maculatae* (S. F. Blake) Panero and E. Schilling, *V.* ser. *Brevifoliae* S. F. Blake and *V.* ser. *Pinnatilobatae* S. F. Blake, all of which share the woody habit and subsessile, glandular, foliar trichomes, and all of which occur in mainland Mexico. *Viguiera* sect. *Maculatae* differs by having phyllaries in which the herbaceous apex is only gradually narrowed from the indurate base, pappus awns that are broad and often paleaceous, habit generally more robust as large shrubs or small trees, and capitulescences that have mostly opposite paracladia (Panero and Schilling 1988). *Viguiera* ser. *Brevifoliae* (with which *V. microphylla* shares a remarkable superficial similarity of habit and appearance) differs by having solitary heads and phyllaries in which the terminal herbaceous portion is very short and not narrowed abruptly. *Viguiera* ser. *Pinnatilobatae*, which Blake (1918) felt was somewhat similar because of its quite similar phyllaries, differs by having pinnately lobed leaves and epappose achenes.

The two species of *V.* ser. *Viguiera* that have been excluded to leave *V.* subg. *Bahiopsis* can be readily distinguished from it and are probably not closely related to the latter (or to each other). The type species of the genus, *V. dentata*, has phyllaries similar to those of *V.* subg. *Bahiopsis*, which led Blake (1918) to group it in the same series with taxa of *V.* subg. *Bahiopsis*. But *V. dentata* is herbaceous (or sometimes suffruticose at the base, but not shrubby), lacks foliar subsessile glands, and has pubescent staminal filaments. When viewed in living material, phyllaries of the other species, *V. potosina* S. F. Blake, appear to be different in being primarily herbaceous throughout and not abruptly narrowed above the base, and *V. potosina* is also distinguished from subg. *Bahiopsis* by its herbaceous habit, lack of foliar subsessile glands, and elongate, tapering style branches. The relationships of *V. potosina* are unclear, but may lie with certain taxa of *V.* ser. *Grammatoglossae* S. F. Blake, such as *V. ovata* (A. Gray) S. F. Blake, *V. rhombifolia* (Robinson & Greenm.) S. F. Blake, and *V. sessilifolia* DC.

## MORPHOLOGY AND RELATIONSHIPS

The diploid species of *V.* subg. *Bahiopsis* are well distinguished from one another by vegetative features including plant size and leaf size, shape, margin, arrangement, and pubescence. Reproductive characteristics are more uniform within the subgenus, and differences are primarily in size of parts and in distribution of certain types of trichomes. The capitulescence of all species is of the monochasial thyrsoïd type (Panero and Schilling 1988), with paracladia primarily alternate in arrangement; there is variation in number of



heads per capitulescence. Variation in head size and shape is correlated with differences in pale shape: cylindric to hemispheric heads are associated with ovate pales; vase-shaped heads have lanceolate to rectangular pales.

The morphological traits that distinguish members of *V.* subg. *Bahiopsis* from one another fail to provide information on phylogenetic relationships within the group. Cladistic analyses of these data (not shown) yield trees with such a high level of homoplasy that little confidence can be placed in them. Flavonoid data appear to be more valuable for cladistic analysis (Schilling 1989) and together with selected morphological characters indicate three clades within the subgenus: one formed by *V. carterae*, *V. similis*, and *V. tomentosa*; a second by *V. lanata*, *V. microphylla*, and *V. subincisa*; and a third by *V. laciniata*, *V. parishii*, and *V. reticulata*. However, the relationships among these clades are not resolved by flavonoid data. Chloroplast DNA data (Schilling and Jansen 1989) also fail to provide any phylogenetically informative characters for this group.

Morphological observations combined with flavonoid data provide insight into genomic relationships between diploid and polyploid species. The morphological similarity of the hexaploid, *V. triangularis*, to the diploid, *V. parishii*, provides compelling evidence of a genomic relationship. Differences in flavonoid profiles suggest that *V. triangularis* is an allopolyploid; most of the compounds not shared with *V. parishii* are observed in the diploid, *V. microphylla*, suggesting that it has also contributed a genome (Schilling 1989). The other hexaploid, *V. chenopodina*, is more similar morphologically and chemically to *V. microphylla*, suggesting that its genomic content may differ slightly from that of *V. triangularis*. Morphology, particularly size of floral parts and pubescence, indicates that the octoploid, *V. deltoidea*, may contain genomes from *V. chenopodina* and the diploid, *V. tomentosa*.

#### GEOGRAPHICAL DISTRIBUTION

The geographical range of each species of *V.* subg. *Bahiopsis* is shown in Figures 1 and 2, which are based on records in herbaria. A list of the specimens examined is available from the author on request.

The diploid species of *V.* subg. *Bahiopsis* exhibit a series of parapatric distributions, ranging from the Mojave Desert in the north to the Cape Region of Baja California Sur (Fig. 1). The probable relatively recent origin of xeric habitats in this region (Axelrod 1958, 1979) and the mainland Mexico distribution of the related elements of *Viguiera* suggest that the subgenus may be an example of an element of the Madro-Tertiary geoflora that has diversified during the relatively recent cycle of xerification that has produced the south-



western deserts. Species may have originated from a more widespread ancestor that occurred in this area through habitat restriction during alternating mesic and xeric climatic cycles.

Polyploid species are sympatric with one or more diploid species and in some cases occupy areas where diploids are absent (Figs. 1, 2). This suggests that the polyploids have either greater colonizing ability or, more likely, wider habitat tolerance than the diploids. For example, the hexaploid, *V. triangularis*, occupies a wide area spanning the ranges of the diploids, *V. laciniata*, *V. lanata*, *V. microphylla*, and *V. carterae* (Figs. 1, 2). Another example is the restriction of the diploid, *V. subincisa*, to offshore Pacific islands compared to the sympatric hexaploid, *V. chenopodina*, which occurs widely on the mainland as well.

#### TAXONOMIC TREATMENT

**Viguiera** Kunth subg. **Bahiopsis** (Kellogg) E. Schill., stat. nov.—*Bahiopsis* Kellogg, Proc. Calif. Acad. 2:35, 1863.—TYPE: *Viguiera lanata* (Kellogg) A. Gray.

Frutescent or shrubby perennials. Leaves alternate or opposite, entire to toothed or incised (but not lobed), with subsessile, glandular, flavonoid-containing trichomes on abaxial and sometimes also on adaxial surface. Capitulescence monochasial thyrsoïd, usually of multiple capitula and with paracladia arranged alternately. Phyllaries with ovate to lance-ovate, indurated base and abruptly narrowed, herbaceous apex. Ray corollas yellow; ray ovaries trigonal with a pappus consisting of a scale at each of the three terminal angles. Disk flowers yellow, tubular-funnelform, with 5 veins, one leading to each sinus; anther appendages lanceolate, with subsessile glands on abaxial surface (except *V. lanata*); staminal filaments and connectives glabrous; styles lacking papillae or trichomes below branch point, the branches acute and exappendiculate; achenes with a pappus of two awns and intermediate scales. Chromosome base number,  $x=18$ .

#### ARTIFICIAL KEY TO THE SPECIES OF *VIGUIERA* SUBGENUS *BAHIOPSIS*

- A. Leaves incised or lacinate-toothed; abaxial surface of leaves either shiny with resin or with enlarged trichome bases that are conspicuously whitened when dry.
  - B. Stem below capitulescence scabrous; abaxial surface of leaves often shiny with resin; leaves lanceolate to lance-ovate, usually less than 40 mm long. . . . . 4. *V. laciniata*
  - B. Stem below capitulescence glabrous or with remote hairs; abaxial surface of leaves dull, often with enlarged trichome bases that are conspicuously whitened when dry; leaves ovate, larger ones more than 40 mm long. . . . . 9. *V. subincisa*
- A. Leaves serrate or entire, but not incised or lacinate-toothed; abaxial surface of



leaves variously glabrate, hispid, hirsute, sericeous, lanate or canescent, but not shiny with resin (although shiny, sessile glandular trichomes may be present) and not with enlarged trichome bases that are conspicuously whitened when dry.

C. Leaves few and primarily crowded together at base of stem, capitulescences subscapose; leaf blade oval to suborbicular, more than 25 mm wide, apex rounded, margin subentire; leaves and lower stem densely lanate, the trichomes long and interwoven; involucre more than 15 mm wide at flowering. .... 5. *V. lanata*

C. Leaves not crowded together at base of stem, capitulescences not subscapose; leaf blade oval, elliptical, ovate, cordate or deltate, 5–80 mm wide; leaves variously scabrous, hirsute, tomentose, canescent or sericeous, but not densely lanate; involucre 8–20 mm wide at flowering.

D. Leaves canescent, silvery or gray on both surfaces (sometimes only beneath in *V. chenopodina*), the trichomes short and closely crowded, with bases at most only slightly tuberculate; leaf margins usually entire (sometimes serrate in *V. chenopodina*).

E. Leaf blade less than 2 cm long; leaves alternate; plants less than 1 m tall; phyllaries less than 5 mm long and apiculate, the herbaceous apex much shorter than the indurate base. .... 6. *V. microphylla*

E. Leaf blade usually more than 2 cm long; leaves (except uppermost) opposite; plants usually more than 1 m tall; larger phyllaries more than 5 mm long and caudate, the herbaceous apex at least half as long as the indurate base. .... 2. *V. chenopodina*

D. Leaf adaxial surface scabrous to hirsute or silvery sericeous to subtomentose, but not canescent, the trichomes various, short to long and with bases tuberculate or not, abaxial surface tomentose, hispidulous-pilosulous, hispidulous, or strigillose; leaf margin margin toothed or entire.

F. Leaves silvery appressed-sericeous adaxially and very strongly reticulate abaxially, the margin usually entire; phyllaries less than 5 mm long. .... 8. *V. reticulata*

F. Leaves usually subtomentose, scabrous, or hirsute adaxially, or if sericeous adaxially, then leaf margin serrate; larger phyllaries usually more than 5 mm long.

G. Leaf blades with adaxial surface silky-sericeous to subtomentose, the trichome bases only slightly tuberculate if at all, and abaxial surface densely tomentose.

H. Achenes 4–5 mm long; plants often more than 3 m tall. .... 11. *V. tomentosa*

H. Achenes 2–3 mm long; plants less than 2 m tall.

I. Pappus persistent; pales less than 6.5 mm long and generally covering less than half of the disk corolla throat. .... 2. *V. carterae*

I. Pappus deciduous; pales more than 6.5 mm long and generally covering more than half of the disk corolla throat. ... 10. *V. similis*

G. Leaf blades with adaxial surface scabrous to hirsute, the trichome bases often conspicuously tuberculate, and abaxial surface hispidulous-pilosulous, hispidulous, or strigillose.

J. Pales 8–15 mm long; achenes 3.5–5.5 mm long; leaves softly and densely hispidulous-pilosulous abaxially, at least when first produced. .... 3. *V. deltoidea*

J. Pales 5–8 mm long; achenes 2.5–4.0 mm long; leaves hispidulous or strigillose abaxially.

K. Larger leaves usually more than 3.5 cm long; capitulescence usually of 3 or more heads; pappus awns 2; plants usually more than 13 dm tall. .... 12. *V. triangularis*



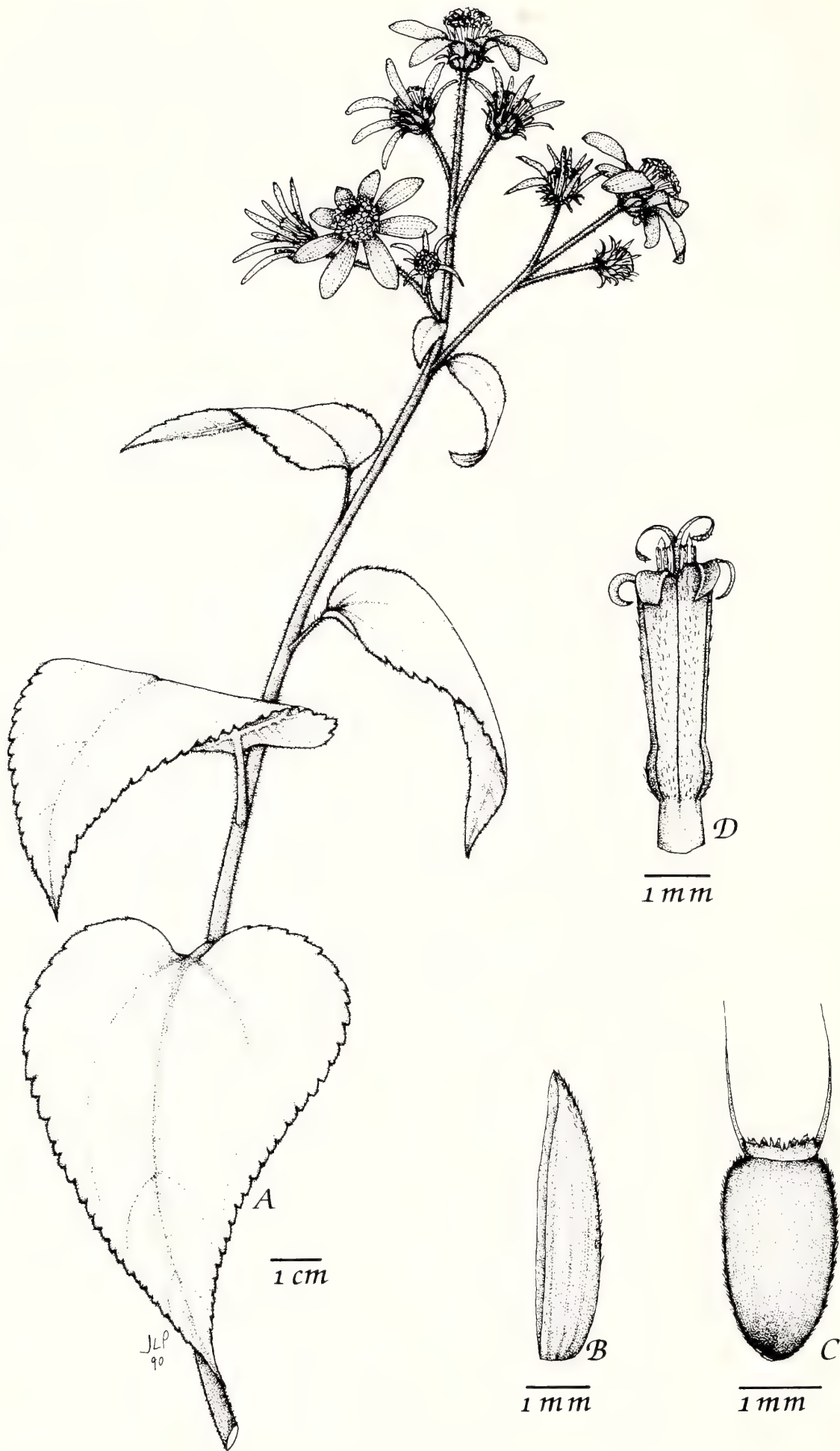
- K. Leaves usually less than 3.5 cm long; capitulescence of 1(–3) heads; pappus awns 2 or 3; plants usually less than 13 dm tall. . . . . 7. *V. parishii*

1. ***Viguiera carterae*** E. Schill., sp. nov. (Fig. 3).—TYPE: MEXICO, Baja California Sur, Sierra de La Giganta, Mesa de San Gerónimo, northerly from Rancho Viejo (on road from Loreto to San Javier), 25°58'–26°N, 111°32'–34'W, 1080 m, 9 May 1966, *A. Carter 5140* (holotype, MEXU!; isotypes, TENN!, UC!, others to be distributed).

*Viguiera tomentosa accedens sed capitula, floribus disci, et achae-niis minoribus.*

Shrub 5–18 dm tall. Stems terete, brown, densely villous when young, becoming glabrescent with age, trichomes white, multicellular, tapered, from narrow base, 0.8–1 mm long. Leaves all opposite, or sometimes opposite at base and alternate above; petioles 4–15 mm long, densely villous; blades deltate, 35–100 mm long, 15–90 mm wide, apex acuminate, base usually cordate, margin dentate, abaxially densely villous, trichomes as on stem, subsessile glandular trichomes confined to abaxial surface, barely visible through dense pubescence, adaxially sericeous, trichomes stiff, white, multicellular from narrow base, 0.5–0.8 mm long. Capitulescence monotelic, composed of a longer (usually), terminal dichasium and usually one or more pairs of lateral dichasia that arise from successively lower nodes, 1–20 heads, peduncles 0.5–4 cm long, densely villous. Heads subcylindric, 3–4 cm across (from tips of rays); disk 8–12 mm in diameter, moderately convex; phyllaries 14–20 in 2(–3) graduated series, 5–9 mm long, base ovate, indurated, 2.5–3.5 mm long, 1.5–2 mm wide, abaxially sparsely to moderately villous, apex linear, herbaceous, abruptly narrowed above base, 2.5–6.5 mm long, abaxially densely villous; pales lance-ovate, conduplicate, 4–6.5 mm long, 1.5–2 mm wide, inner usually larger than outer, stramineous with few dark-brown bands, abaxial surface sparsely–moderately pubescent, adaxial surface glabrous, apex deltate, somewhat concave and narrowed to acute tip. Ray flowers 7–10, corolla golden yellow, limb 16–19 mm long, 6–8 mm wide, oval-lanceolate, abaxial surface sparsely pubescent along veins and with numerous subsessile glandular trichomes between veins, apex bifid or trifid, tube 1.6–1.9 mm long; ray ovary 2 mm long, 0.4–0.5 mm wide, trigonal, sparsely pubescent, pappus of 3 small scale-like awns on angles. Disk flowers 55–70; corollas yellow, slightly campanulate, tube 0.3–0.5 mm long, 0.4–0.5 mm wide, wider at base, pubescent, throat 3.5–4.5 mm long, 0.8–1.2 mm wide, narrowed above slightly bulbous base and then widening gradually toward junction with lobes, sparsely pubescent, most or all of throat protruding beyond pales, lobes deltate, golden







yellow, 0.3–0.5 mm long, abaxially pubescent, anthers 1.9–2.3 mm long, reddish-brown, appendages 0.4–0.6 mm long, style about 7 mm long, branches 0.8–1.1 mm long; disk achenes ovate, biconvex, 2–2.4 mm long, densely pubescent on angles and sparsely pubescent on black surface with silvery-gray, biseriate trichomes (Zwilling-shaare), pappus of 2 awns and intermediate scales, awns slender, subequal, somewhat curved inward, 1.3–1.5 mm long, scales 0.2–0.4 mm long. Chromosome number,  $n$ =ca. 18.

PARATYPES: MEXICO, Baja California Sur: type locality, 9 Sep 1965, *A. Carter 5041* (MEXU!, TENN! UC!, others to be distributed); 2 Mar 1984, *E. E. and E. M. Schilling 48* (TENN!, MEXU!); Sierra Giganta, Arroyo Hondo, 15 Dec 1938, *H. S. Gentry 4158* (ARIZ!, DS-2!).

This species closely resembles *V. tomentosa* and *V. similis*; all three species exhibit similar leaf shape and pubescence and also lack pubescence on the tube of the disk flowers. It differs from *V. tomentosa* in the smaller size of the heads and most parts of the flowers. In addition, plants of *V. carterae* do not attain as large a size as those of *V. tomentosa*. The collections of *V. carterae* are all from the Sierra de La Giganta region, which is of volcanic origin, whereas *V. tomentosa* and *V. similis* occur in the older granitic soils of the more southerly Cape Region (Fig. 1). It appears that *V. carterae* is restricted to a few peaks, where it may receive significant moisture through fog. Its limited distribution suggests that it may be a relict species adapted to more mesic conditions and isolated in a shift toward a more xeric climate. The population at the type locality when visited in 1984 was fairly extensive but the area had been dry and the plants were quiescent; material for floral measurements and a chromosome count was obtained from plants grown from seed at the University of Tennessee greenhouse facility (these plants grew for three years before flowering for the first time). The species is named in honor of Annetta Carter, of the University of California at Berkeley, who has made significant contributions to the knowledge of the flora of the Baja California Peninsula, and who drew the attention of the author to the existence of this species.

2. *Viguiera chenopodina* E. Greene, Leaf. Bot. Observ. Crit. 2:154. 1911; *V. deltoidea* A. Gray var. *chenopodina* (E. Greene) S. F. Blake, Contr. Gray Herb. 18:91. 1918.—TYPE: MEXICO, “Lower California” [Baja California Sur]: “from Santo Domin-

---

←

FIG. 3. *Viguiera carterae*. A. Flowering branch. B. Pale. C. Achene. D. Disk corolla. Based on a greenhouse plant grown from *E. E. and E. M. Schilling 48*.



go to Matancita", 14–15 Nov 1905, *E. W. Nelson and E. A. Goldman* 7277 (holotype, US!; isotype, GH!).

*Viguiera deltoidea* A. Gray var. *townsendii* Vasey & Rose, Proc. U.S. Natl. Mus. 13:148. 1890.—TYPE: MEXICO, "Lower California" [Colima]: Socorro Island, Mar 1889, *C. H. Townsend s.n.* (holotype, US!).

Shrubs 1–3 m high; petioles 3–13 mm long; leaf blades 12–56 mm long, 10–36 mm wide; phyllaries 3–7 mm long, 1–1.5 mm wide; pales 6.5–8 mm long, glandular; disk corollas 4–5.5 mm long; achenes 3.5–4 mm long; pappus of 2 awns 2.9–3.5 mm long and 2 lacerate-erose scales 1.2–1.7 mm long; chromosome number,  $n=54$ .

*Representative specimens.* MEXICO, Baja California Sur: Arroyo Tabor, W of Puerto Escondido, 18 Mar 1961, *A. Carter and H. Sharsmith* 4251 (DS, MEXU, SD, UC); 11 mi N of Salada (Medano), 17 Feb 1947, *L. Constance* 3156 (DS, GH, LL, MEXU, UC); about 76 km N of La Paz, road to Cd. Constitución, 1 Mar 1984, *E. E. and E. M. Schilling* 39 (MEXU, TENN); Colima: Isla Socorro, Mar–Jun 1987, *A. W. Anthony* 389 (DS, GH, MEXU, UC).

Typical material of *V. chenopodina* has small, entire or subentire leaves that are grayish-green on both surfaces due to the dense, appressed pubescence, with trichomes on the upper surface usually having bases that are only slightly expanded. The leaf shape and pubescence are very similar to those of the diploid species, *V. microphylla*, although the two species are easily distinguished by the larger leaves and heads in *V. chenopodina*.

*Viguiera chenopodina* is one of two hexaploid taxa that have been considered to be varieties of *V. deltoidea* (Blake 1918). Recognition of the occurrence of polyploidy has provided an explanation for the existence of the puzzling morphological variation in this complex, but does not resolve all of the taxonomic problems. There is some intergradation between *V. chenopodina* and the other hexaploid, *V. triangularis*, and it could be argued that they might be better recognized as infraspecific taxa. The differences involve the same types of vegetative features that distinguish the diploid species, however, and there are also differences in external flavonoid aglycones (Schilling 1989). There are also differences in the pigmentation and degree of glandularity of the pales: those of *V. chenopodina* lack the dark pigmentation and are conspicuously glandular, especially at the apex (these sessile glandular trichomes tend to be deciduous, making this difficult to evaluate in fruiting material), whereas those of *V. triangularis* tend to have dark pigmentation at the apex and along the keel and have only a few glandular trichomes. The typical extremes are quite distinct over fairly large areas, with *V. chenopodina* found throughout the Llano de Magdalena (the flat plain that extends west from the Sierra de La Giganta to the Pacific Ocean) and *V.*



*triangularis* found further to the north from the Sierra San Pedro Mártir through the Central Desert (Fig. 2). Plants with intermediate combinations of traits for leaf size and shape and pale pigmentation and glandularity occur in several places, most conspicuously in the Sierra de La Giganta region and on some of the offshore islands in the Gulf of California and the Pacific Ocean. It is likely that each island population is reproductively isolated and genetically distinct but it seems of dubious value to give them different names; because they differ from both, assignment of these to *V. chenopodina* or *V. triangularis* is also somewhat arbitrary. The plants from Socorro Island (Levin and Moran 1989) have a uniform and slightly different appearance and have been named as *V. deltoidea* var. *townsendii*, but because they are also hexaploid and appear quite similar to plants that occur on some of the islands nearer to Baja California they are here placed in *V. chenopodina*.

3. *Viguiera deltoidea* A. Gray, Proc. Amer. Acad. Arts 5:161. 1861–1962.—TYPE: MEXICO, “Lower California” [Baja California Sur], “Cape San Lucas, & c.”, Aug 1859–Jan 1860, *L. J. Xantus* 60 (lectotype, here designated, GH!; isolectotypes, US!, K!).

*Viguiera deltoidea* A. Gray var. *tastensis* Brandegee, Zoe 5:161. 1903.—TYPE: MEXICO, “Lower California” [Baja California Sur], Sierra El Taste, Nov 1902, *T. S. Brandegee* s.n. (holotype, UC!; isotype, GH!).

All of the syntypes of *V. deltoidea* bear the annotation “n.sp.”, apparently by Gray, so there is no obvious holotype. Because the specimen at GH is in the best condition it is designated as lectotype.

Shrubs or small trees 1–4 m high; petioles 8–16 mm long; leaf blades 37–96 mm long, 35–80 mm wide; phyllaries 7–10 mm long, 1–2 mm wide; pales 8–15 mm long, glandular; disk corollas 4.5–6 mm long; achenes 3.5–5 mm long; pappus of 2 awns 3.5–4 mm long and 2 lacerate-erose scales 1–2 mm long; chromosome number,  $n=72$ .

*Representative specimens.* MEXICO, Baja California Sur: El Taste ridge, S side of La Carrerita, 9 Nov 1955, *A. Carter and F. Chisaki* 3508 (DS, GH, MEXU, SD, UC); 2 mi NE of Todos Santos, 23 Feb 1947, *L. Constance* 3190 (DS, GH, MEXU, UC), 8 km S of Pescadero, 15 Jan 1959, *R. Moran* 7024 (ARIZ, DS, GH, MEXU, SD); along Hwy 19 just S of Colonia Plutarco Elias Calles and ca. 39 mi N of Cabo San Lucas, 29 Feb 1984, *E. E. and E. M. Schilling* 21 (MEXU, TENN).

Chromosome studies (Schilling and Schilling 1986) indicate that plants classified by Blake (1918) as varieties of *V. deltoidea* sensu lato form a polyploid complex, and these varieties are here recognized individually as species. Examination of the type of *V. deltoidea*



indicates that this name applies to a taxon usually identified as *V. deltoidea* var. *tastensis*; specimens mistakenly identified in the past as var. *deltoidea* (or var. *genuina*) are here referred to *V. triangularis*.

*Viguiera deltoidea* as delimited here is restricted to the Cape Region (Fig. 2), where it is sympatric with (and may occasionally be found growing next to) *V. tomentosa*. The two species are easily distinguished by leaf pubescence as described in the key. Similarities in robust habit and lessened pubescence on disk corollas point to the hypothesis that *V. deltoidea* contains a genome from *V. tomentosa*. Like *V. tomentosa*, *V. deltoidea* appears to be capable of blooming throughout the year.

*Viguiera deltoidea* is quite similar morphologically to *V. triangularis*, as evidenced by the fact that Blake (1918) placed material of the latter taxon under the name of *V. deltoidea*. It is easier to distinguish living plants of these species, where the generally larger and more robust features and habit of *V. deltoidea* are obvious, than herbarium material. In general, *V. deltoidea* has slightly longer achenes, pales and pappus scales than does *V. triangularis*, in addition to having a denser and softer pubescence on the abaxial leaf surface.

4. *Viguiera laciniata* A. Gray in Torrey, Bot. Mex. Bound. 89. 1859.—TYPE: USA, California, Rancho Gamacha, east of San Diego, Sep 1855, A. Schott s.n. (holotype, GH!).

Shrubs to 13 dm high; petioles 3–7 mm long; leaf blades 15–43 mm long, 6–25 mm wide; phyllaries 4.5–7 mm long, 1.8–3 mm wide; pales 5.5–7.3 mm long, glandular or resinous; disk corollas 3.5–4.5 mm long; achenes 2–3.5 mm long; pappus of 2 awns 1.7–2.5 mm long and 2 lacerate-erose scales 0.4–0.5 mm long, somewhat deciduous; chromosome number,  $n=18$ .

*Representative specimens.* MEXICO, Baja California Norte: Ensenada, Mar–Jun 1897, A. W. Anthony 181 (DS, GH, MEXU, MO, POM, SD, UC); 2 mi N of Parador Santa Inéz, 26 Mar 1979, J. R. and C. G. Reeder 7107 (ARIZ, ENCB, TEX, UC); 22 mi E of Hwy 1 on road to Bahía de Los Angeles, 11 Mar 1984, E. E. and E. M. Schilling 109 (MEXU, TENN); Sonora, in canyon at Punta Cirio, 14 Apr 1979, J. E. Bowers and S. P. McLaughlin 1619 (ARIZ); USA, California: San Diego Co., near Potrero, 5 May 1903, L. Abrams 3450 (DS, GH, MO, POM, UC).

This species is quite distinctive based on the laciniate leaf shape and the resinous nature of the herbage; it also has a distinctive assemblage of foliar flavonoid aglycones relative to other members of *V.* subg. *Bahiopsis* (Schilling 1989). Although there is a superficial similarity of leaf shape to *V. subincisa*, there are no other shared



features that suggest a close phyletic relationship between these species. The species remains remarkably constant over its range from southern California to the Central Desert region of Baja California, as well as a disjunction to the state of Sonora (Fig. 1), although plants from the southern areas tend to be slightly larger than those from the north.

5. *Viguiera lanata* (Kellogg) A. Gray, Proc. Amer. Acad. Arts 17: 218. 1882; *Bahiopsis lanata* Kellogg, Proc. Calif. Acad. Sci. 2: 35. 1863.—TYPE: MEXICO, "Lower California" [Baja California Sur], Cedros Island, no date, *J. A. Veatch s.n.* (holotype, CAS!).

The holotype is noteworthy in consisting of a specimen cut from a larger sheet and reglued to a standard size herbarium sheet. The other side of the original specimen sheet is in GH and contains two specimens, also of *V. lanata*: *L. Belding s.n.*, 1881; and *L. W. Street s.n.*, no date. In addition to the type specimen, which is stamped no. 53952 of CAS, a second collection is glued to the type sheet: "Rev. E. L. Greene s.n., 1 May 1885, Lower California, Cedros Island," CAS, no. 53951. A previous type annotation label has been incorrectly placed across the Greene collection.

Suffruticose perennials with flowering stems to 5.5 dm high; petioles 9–60 mm long; leaf blades 25–100 mm long, 23–80 mm wide; phyllaries 6–10 mm long, 1–3 mm wide; pales 7–8 mm long, glandular; disk corollas 3.5–5 mm long; achenes 2.7–3.8 mm long; pappus of 2 awns 1.8–2.2 mm long and 2 lacerate-erose scales 0.8–1.2 mm long; chromosome number,  $n=18$ .

*Representative specimens.* MEXICO, Baja California Sur: Arroyo de las Casitas, 8 mi above mouth, 9 Feb 1973, *R. Moran and J. Reveal* 19970 (ARIZ, ASU, GH, MICH, SD, UC, US); 7 mi S of Punta Eugenia, road to Bahía Tortugas, 8 Mar 1984, *E. E. and E. M. Schilling* 88 (MEXU, TENN); I. Cedros, W of Cedros village, 14 Apr 1963, *R. Moran* 10604 (RSA, UC); I. Natividad, *R. Moran* 15138 (SD, UC, US).

*Viguiera lanata* occurs at the very tip of the Vizcaino Peninsula and on the adjacent offshore Isla Cedros and Isla Natividad (Fig. 1). Where it occurs on the mainland it is the dominant shrub on low rounded hills. The species has an unmistakable appearance with its long scapose capitulescences rising well above the compact mounds of silvery-gray foliage. In superficial aspect it looks much like an *Encelia* and in fact presents a striking example of apparent convergence with elements of *E. farinosa* that occur elsewhere in the Baja California Peninsula. Details of the involucre, pales, and achenes confirm its placement in *V.* subg. *Bahiopsis*. The dense pubescence



and oval leaves are reminiscent of *V. chenopodina*, but the different character of the trichomes and habit between the species suggest this to be convergence rather than evidence of shared ancestry.

6. *Viguiera microphylla* Vasey & Rose, Proc. U.S. Natl. Mus. 11: 535. 1890.—TYPE: MEXICO, "Lower California" [Baja California Sur], Lagoon Head, "40 miles back from the ocean", 6–15 Mar 1889, *E. Palmer* 270 (holotype not located); same locality and date, *E. Palmer* 802 (neotype, here designated, US!; isoneotypes, ARIZ! US!, GH!).

The type listed by Vasey and Rose is not among the collections at US or GH, and it was not found by Blake (1918). According to McVaugh (1956), the specimens collected by Palmer at the Lagoon Head locality comprised numbers 651–958, a series which would obviously not include the number 270 cited by Vasey and Rose. Hence, *E. Palmer* 802 may prove to be identical to *E. Palmer* 270 and represent a lectotype. Another collection of *V. microphylla* also from this same locality and date is *E. Palmer* 880.

Shrubs 5–10 dm high; petioles 2.5–6 mm long; leaf blades 7–19 mm long, 5–14 mm wide; phyllaries 1.5–4.3 mm long, 0.8–1.1 mm wide; pales 4.5–6.5 mm long, glandular; disk corollas 3–4 mm long; achenes 3.5–4 mm long; pappus of 2 awns 1.6–2 mm long and 2 lacerate-erose scales 0.9–1.3 mm long; chromosome number,  $n=18$ .

*Representative specimens.* MEXICO, Baja California Norte: 15 mi E of Hwy 1, road to Bahía de los Angeles, 10 Mar 1984, *E. E. and E. M. Schilling* 103 (MEXU, TENN); ca. 30 mi N of Guerrero Negro, dunes S of Miller's Landing, 25 Mar 1974, *G. L. Webster and K. Steiner* 19655 (ARIZ, LL, MEXU, MO, SD); Baja California Sur: Sebastián Vizcaíno, 12 Nov 1968, *J. Rzedowski* 26478 (ARIZ, DS, ENCB, MEXU, POM); 6 mi N from Cuarenta, road between San Ignacio and La Purísima, *J. H. Thomas* 8356 (DS, ENCB, POM, US).

*Viguiera microphylla* occurs in the Vizcaíno Desert region in the central part of the Baja California Peninsula (Fig. 1) as part of the microphyllous shrub association. It has the most diminutive leaves and heads of the subgenus, but the pales and achenes are of average size for the group. It appears to be successful along the margins of Highway 1, with plants less common as one moves away from the roadway.

Blake (1918) noted the resemblance between *V. microphylla* and *V. chenopodina* and was of the opinion that additional collections might bridge the gap between the two. Chromosome studies (Schilling and Schilling 1986) indicate that these represent diploid and hexaploid levels, respectively, and suggest that the morphological resemblance may indicate that *V. chenopodina* includes one or more



genomes from *V. microphylla*. The species are distinguished by the smaller leaves, heads and habit of *V. microphylla*.

7. *Viguiera parishii* E. Greene, Bull. Torrey Bot. Club 9:15. 1882; *Viguiera deltoidea* A. Gray var. *parishii* (E. Greene) Vasey & Rose, Contr. U.S. Nat. Herb. 1:71. 1890.—TYPE: USA, California, [San Diego Co.] San Luis Rey, 1881, *S. B. and W. F. Parish* 963 (lectotype, here designated: DS!; isolectotype: GH!).

Shrubs to 13 dm high; petioles 3–6 mm long; leaf blades 15–35 mm long, 13–35 mm wide; phyllaries 3–9 mm long, 0.8–1.5 mm wide; pales 5–6 mm long, eglandular; disk corollas 3.5–5 mm long; achenes 2.7–3.8 mm long; pappus of 2(–3) awns 2–3 mm long and 2 lacerate-erose scales 0.5–1 mm long; chromosome number,  $n=18$ .

*Representative specimens.* MEXICO, Baja California Norte: 6 km SSE of El Rodeo, 14 Sep 1977, *R. Moran* 24716 (SD, UC); Sonora: 6 mi N of Quitovac on road to Sonoyta, 12 Mar 1936, *D. D. Keck* 4119 (DS, GH, POM, UC); USA, Arizona: Maricopa Co., N of Scottsdale, road to Pinnacle Peak, 17 Mar 1984, *E. E. and E. M. Schilling* 140 (TENN); California: Riverside Co., Eagle Mts., 18 May 1941, *A. M. Alexander and L. Kellogg* 2196 (ARIZ, DS, GH, LL, POM, UC); Nevada: Clark Co., Searchlight, 2 Sep 1953, *P. Raven* 6322 (DS).

Type material for this species was not found at NDG, so the specimen at DS from the Parish herbarium is designated as lectotype. A number of specimens under this collection number, but collected apparently at different places and dates, are to be found in various herbaria.

As discussed below, it is difficult to distinguish *V. parishii* and *V. triangularis* from herbarium material. For this reason, it has been difficult to discern the limits of the ranges of these species to determine whether or not they overlap (Figs. 1, 2). In the course of my own field studies, no plants of *V. triangularis* were seen in the southwestern U.S., and all of the plants of this kind collected near and along Highway 3 between Ensenada and San Felipe were of *V. triangularis*. Any overlap between the two species would thus have to occur in extreme northern Baja California, an area where few specimens of this group have been collected.

8. *Viguiera reticulata* S. Watson, Amer. Naturalist. 7:301. 1873.—TYPE: USA, California, [Inyo Co.], Telescope Mts., 1871, *G. M. Wheeler s.n.* (holotype, GH!).

Shrubs 5–15 dm high; petioles 3.5–17 mm long; leaf blades 28–60 mm long, 23–45 mm wide; phyllaries 3–5 mm long; pales 4–5.5 mm long, glandular; disk corollas 3–4 mm long; achenes 2.5–4 mm



long; pappus of 2 awns 1.5–2.8 mm long and 2 scales 0.6–1 mm long; chromosome number,  $n=18$ .

*Representative specimens.* USA, California: Inyo Co., Wild Rose Station, Panamint Range, 24 Mar 1940, *F. W. Gould* 979 (ARIZ, DS, GH, MO, UC, US); Death Valley National Monument, Grotto Canyon, 23 Mar 1983, *E. Schilling and L. Rieseberg* 83-16 (TENN); San Bernardino Co., Sheep Springs Canyon, 24 Mar 1964, *C. L. Hitchcock and C. V. Muhlick* 23296 (DS, UC); Nevada: Nye Co, Bare Mtn., base of SW face, 19 Jun 1969, *J. Beatley* 9054 (DS, RSA).

This species is restricted to the Mojave Desert in areas near Death Valley (Fig. 1), where it occurs at mid-elevations in grottoes and canyons. The only other geographically proximal species of subg. *Bahiopsis* is *V. parishii*, from which *V. reticulata* differs in having larger leaves (the leaf blade more than 3 cm long) that are more prominently reticulate beneath and that have a denser, silvery pubescence on the upper surface with individual trichome bases only slightly enlarged. This species has a pronounced vase-like shape to its heads, and its prominent anther collars and almost ovoid, flattened anther appendages are distinctive within the subgenus.

9. *Viguiera similis* Brandege, Zoë 5:260. 1908; *Helianthus similis* (Brandegee) S. F. Blake, Contr. Gray Herb. 54:189. 1918.—  
TYPE: MEXICO, “Lower California” [Baja California Sur], Sierra de San Francisquito, 18 Oct 1890, *T. S. Brandege* s.n. (holotype, UC!).

Shrubs (?) to 1.5 m high; petioles 8–20 mm long; leaf blades 65–160 mm long, 26–90 mm wide; phyllaries 5–10 mm long, 1–1.5 mm wide; pales 6.5–7.5 mm long, eglandular; disk corollas 4–4.5 mm long; achenes 2.5–3 mm long; pappus of 2 deciduous awns 2.4–2.7 mm long; chromosome number unknown.

*Representative specimens.* MEXICO, Baja California Sur: Sierra La Laguna, S of Pico La Aguja, 22 Oct 1977, *D. E. Breedlove and D. I. Axelrod* (DS, MEXU); Sierra de La Laguna, 13 Oct 1941, *B. J. Hammerly* 366 (DS, POM. SD); El Taste Ridge, S side of La Carrerita, 9 Nov 1955, *A. Carter and F. Chisaki* 3507 (IND, UC); Sierra de La Laguna, about 15 mi E of Todos Santos, 25 Dec 1973, *P. Somers, F. Bowers, and C. Delgadillo* M. 526 (MEXU, TENN).

Blake (1918) transferred this species to *Helianthus* because of its deciduous pappus, a decision that has since generally been followed (Heiser et al. 1969; Wiggins 1980; Rogers et al. 1982). A deciduous pappus has now been shown to occur in several species that clearly belong in *Viguiera*, however, and the close morphological similarity of *V. similis* to *V. tomentosa* and *V. carterae* suggests that it belongs in *V.* subg. *Bahiopsis*. Wiggins (1980) appears to have been incorrect



in indicating that this species is an annual; the label on *Breedlove* and *Axelrod* 43294 describes it as a shrub to 4 ft tall.

*Viguiera similis* is apparently restricted to higher elevations of the Sierra de La Laguna in the Cape Region of Baja California Sur (Fig. 1) where it has been collected relatively few times. Morphologically, this species is quite similar to *V. tomentosa* (Heiser et al. 1969), but differs from it in having smaller achenes that have a deciduous pappus of awns but not scales, in having the base of the leaves more rounded and less cordate, and in apparently being less robust in overall size.

10. *Viguiera subincisa* Benth, Bot. Voy. Sulph. 27. 1884. — TYPE: MEXICO, "Lower California" [Baja California Sur], Magdalena Bay, Oct–Nov 1839, *G. W. Barclay* 3155 (lectotype, here designated, K!; isoelectotypes, BM!, RSA!).

Blake (1918) designated *G. W. Barclay* 3155 and *Hinds* 1841 as cotypes for this species. The specimen of *Barclay* at K lacks a number, but is here designated as lectotype because it is the only cotype that bears both the handwritten annotation "sp.n." and has a "Herb. Hooker" stamp on it to indicate it was available to Benth (C. Jeffrey pers. comm.).

Shrubs to 15 dm high; petioles 10–47 mm long; leaf blades 30–63 mm long, 15–45 mm wide; phyllaries 2.8–3.2 mm long, 0.7–1.0 mm wide; pales 4.5–5.5 mm long, glandular; disk corollas 2.5–3.2 mm long; achenes 2.7–3.2 mm long; pappus of 2 awns 2.3–2.7 mm long and 2 lacerate-erose scales 1.0–1.1 mm long; chromosome number,  $n=18$ .

*Representative specimens.* MEXICO, Baja California Sur: Isla Magdalena, Man-of-War Cove, 23 Apr 1963, *R. Moran* 10814 (MEXU, MICH, SD, UC); Isla Magdalena, just S of Puntarenas, 25 Feb 1984, *E. E. and E. M. Schilling* 3 (MEXU, TENN); Isla Magdalena, S of Puerto Magdalena, 21 Mar 1974, *G. L. Webster and K. Steiner* 19574 (ARIZ, GH, LL, MEXU, MO, SD); Isla Santa Margarita, third beach from W end on N side, 6 Apr 1971, *R. M. Beauchamp* 2115 (SD).

This species is restricted to the volcanic offshore islands, Isla Magdalena and Isla Santa Margarita (Fig. 1). Unlike *V. lanata*, it does not apparently occupy any of the adjacent mainland, which is formed of the much lower Llano de Magdalena. Comments of Blake (1918) and Wiggins (1980) regarding the habit of this species are misleading; *V. subincisa* is a short but distinctly woody shrub. The only other species of *Viguiera* that is sympatric with *V. subincisa* is *V. chenopodina*, which is distinguished by the entire or slightly toothed and minutely but densely pubescent leaves and larger disk flowers and achenes.



11. *Viguiera tomentosa* A. Gray, Proc. Amer. Acad. Arts 5:161. 1861–1862.—TYPE: MEXICO, “Lower California” [Baja California Sur], “Cape St. Lucas, & c.,” Aug 1859–Jan 1860, *L. J. Xantus 61* (lectotype, here designated, GH!; isoelectotype, K!).

Shrubs or small trees to 4 m high; petioles 6–45 mm long; leaf blades 4–13 cm long, 2–11 cm wide; phyllaries 6–9 mm long, 0.8–1.5 mm wide; pales 7–10.5 mm long, eglandular; disk corollas 4.5–6.5 mm long; achenes 3.8–5.7 mm long; pappus of 2 awns 3.2–4.8 mm long and 2 lacerate-erose scales 0.7–1.0 mm long; chromosome number,  $n=18$ .

*Representative specimens.* MEXICO, Baja California Sur: Cape Region, La Hiedra, near headwaters of Arroyo NW of El Encinal, 8 Nov 1955, *A. Carter and F. Chisaki 3470* (DS, MEXU, SD, UC, US); 4 mi SE of Triunfo, 18 Feb 1947, *L. Constance 3161* (DS, GH, LL, MEXU, MO, UC, US); about 5 mi N of Cabo San Lucas on Hwy 19, 28 Feb 1984, *E. E. and E. M. Schilling 19* (MEXU, TENN).

Both of the syntypes are annotated “n.sp.,” apparently by Gray, so there is no obvious holotype. Because the specimen at GH is in better condition it is designated as the lectotype.

*Viguiera tomentosa* is conspicuously larger in most respects than most other species of *V.* subg. *Bahiopsis*. The plants are larger, the achenes are longer, and the capitulescences have more heads. The robust size and numerous heads per capitulescence make *V. tomentosa* resemble more closely the species of *V.* sect. *Maculatae* (Panero and Schilling 1988) than any other species of *V.* subg. *Bahiopsis*.

This species is restricted to the Cape Region (Fig. 1). It apparently is capable of blooming throughout the year. The only species with which it is sympatric is *V. deltoidea*, which is readily distinguished by the less pubescent leaves. The similar and apparently related species, *V. similis*, also occurs in the Cape Region, but only at higher elevations in the Sierra de La Laguna region where *V. tomentosa* is apparently absent. The two species can be distinguished by the smaller achene with its deciduous pappus in *V. similis* and by the larger size of most flower parts in *V. tomentosa*.

12. *Viguiera triangularis* M. E. Jones, Contr. West. Bot. 18:75. 1933.—TYPE: MEXICO, “Lower California” [Baja California Sur], “Arroyo Undo” [=Arroyo Hondo, NW of Loreto at north base of Cerro Giganta], 26 Oct 1930, *M. E. Jones 27710* (lectotype, here designated, POM!; isoelectotypes, DS!, MO!, UC!).

Shrubs 1–2 m high; petioles 5–15 mm long; leaf blades 30–52 mm long, 15–55 mm wide; phyllaries 3–8 mm long, 1–2 mm wide; pales 6–8 mm long, eglandular to sparsely glandular; disk corollas 4–5.6 mm long; achenes 3.1–4.4 mm long; pappus of 2 awns, 2.5–4.0 mm



long and 2 lacerate-erose scales 0.8–1.5 mm long; chromosome number,  $n=54$ .

*Representative specimens.* MEXICO, Baja California Norte: Hwy 1 at Cataviña, 20 Mar 1983, *E. Schilling and L. Rieseberg* 83-9 (MEXU, TENN); 5.5 mi N of El Arrastras, 24 Mar 1960, *I. L. and D. B. Wiggins* 15918 (ARIZ, DS, LL, MEXU); Baja California Sur: Arroyo de La Higuera, NE of Cerro de La Giganta, 9 Oct 1951, *A. Carter and L. Kellogg* 3143 (DS, GH, MEXU, SD, UC).

This name is used for the taxon that has been commonly but erroneously referred to as *V. deltoidea* var. *genuina* (Blake 1918) and *V. deltoidea* var. *deltoidea* (Schilling and Schilling 1986). Blake (1945) pointed out that *V. triangularis* falls within his concept of *V. deltoidea*.

At the northern end of its range (Fig. 2), the hexaploid, *V. triangularis*, is morphologically quite similar to the diploid, *V. parishii*, and there is no single character that always distinguishes them. Generally parts of the hexaploid are slightly larger than those of the diploid, although there is considerable overlap. The ligules of *V. triangularis* typically have more numerous subsessile glands on the lower surface than those of *V. parishii*. Flavonoid aglycone profiles of the two species are quite different, with *V. triangularis* exhibiting all of the compounds of *V. parishii* as well as additional ones (Schilling 1989), suggesting that it is not merely an autopolyploid. In the field the taxa are easily distinguished, with *V. triangularis* a larger, more erect shrub, whereas plants of *V. parishii* tend to be much shorter and more spreading. At the southern end of the range, the distinction between *V. triangularis* and the other polyploids, *V. chenopodina* and *V. deltoidea*, is problematical, as discussed above under the respective species. Specimens from Isla San Pedro Nolasco are atypical in the small head size, but are provisionally placed in *V. triangularis*; as with other samples from islands in the Sea of Cortéz, assignment to a hexaploid species is somewhat arbitrary.

#### ACKNOWLEDGMENTS

I thank the curators of ARIZ, ASU, BM, CAS, DS, GH, ENCB, K, LL, MO, MEXU, NDG, POM, RSA, TEX, UC, and US for the loan of specimens, A. Carter for helpful information on collecting in Baja California and particularly for drawing my attention to *V. carterae*, M. Fuerte O. for leading me to the site of *V. carterae*, V. Bates and C. Jeffrey for supplying information regarding specific type material, G. Levin for collecting material of *V. chenopodina* from Socorro Island, D. Keil for samples of *V. chenopodina*, L. Rieseberg and E. M. Schilling for assistance with field work, J. L. Panero for assistance with morphological analyses, for providing the illustration of *V. carterae*, and for the Spanish translation of the abstract, D. Pinkava, J. Strother, and B. L. Turner for helpful comments on an earlier draft of the paper, and the U.S. National Park Service for permission to collect specimens of *V. reticulata* in the Death Valley National Monument. This research was supported by the U.S. National Science Foundation, Grant BSR-8300023, and by a University of Tennessee Faculty Research Award.



## LITERATURE CITED

- AXELROD, D. I. 1958. Evolution of the Madro-Tertiary geoflora. *Bot. Rev.* (Lancaster) 24:433–509.
- . 1979. Age and origin of Sonoran Desert vegetation. *Occ. Pap. Calif. Acad. Sci.* 132:1–74.
- BLAKE, S. F. 1918. A revision of the genus *Viguiera*. *Contr. Gray Herb.* 54:1–218.
- . 1945. Asteraceae described from Mexico and the southwestern United States by M. E. Jones, 1908–1935. *Contr. U.S. Natl. Herb.* 29:117–137.
- HEISER, C. B., JR., D. M. SMITH, S. B. CLEVENGER, and W. C. MARTIN, JR. 1969. The North American sunflowers (*Helianthus*). *Mem. Torrey Bot. Club* 22(3):1–218.
- LEVIN, G. A. and R. MORAN. 1989. The vascular flora of Isla Socorro, Mexico. *Mem. San Diego Soc. Nat. Hist.* 16:1–71.
- McVAUGH, R. 1956. Edward Palmer: plant explorer of the American West. University of Oklahoma Press, Norman, OK.
- PANERO, J. L. and E. E. SCHILLING. 1988. Revision of *Viguiera* sect. *Maculatae* (Asteraceae: Heliantheae). *Syst. Bot.* 13:371–406.
- RIESEBERG, L. H. and E. E. SCHILLING. 1985. Floral flavonoids and ultraviolet patterns in *Viguiera* (Compositae). *Amer. J. Bot.* 72:999–1004.
- ROGERS, C. E., T. E. THOMPSON, and G. J. SEILER. 1982. Sunflower species of the United States. National Sunflower Association, Bismarck, ND.
- SCHILLING, E. E. 1989. External flavonoid aglycones of *Viguiera* series *Viguiera* (Asteraceae: Heliantheae). *Biochem. Syst. Ecol.* 17:535–538.
- and R. K. JANSEN. 1989. Restriction fragment analysis of chloroplast DNA and the systematics of *Viguiera* and related genera (Asteraceae: Heliantheae). *Amer. J. Bot.* 76:1771–1780.
- and E. M. SCHILLING. 1986. Chromosome numbers in *Viguiera* series *Dentatae* (Compositae). *Syst. Bot.* 11:51–55.
- WIGGINS, I. L. 1980. Flora of Baja California. Stanford University Press, Stanford, CA.

(Received 30 Nov 1989; revision accepted 27 Feb 1990.)

## ANNOUNCEMENT

## MANAGEMENT OF ENDANGERED HABITATS

On Saturday, 27 Oct 1990, Southern California Botanists will hold their 16th annual symposium on the topic of Management of Endangered Habitats. This topic is a follow-up to last year's highly successful symposium on Endangered Plant Communities of Southern California. Speakers will represent various public agencies and/or other organizations responsible for management and restoration of California's endangered habitats.

This program is cosponsored by the Department of Biology at Cal State Fullerton and will be held in the Ruby Gerontology Center on the Cal State Fullerton campus. Registration begins at 8:00 AM. Registration fee is \$10.00 for non-members of SCB, \$8.00 for students, and \$15.00 for members of Southern California Botanists (including renewal of the \$8.00 annual membership). For more information contact Diana Cosand at (714) 773-3548.



A SYSTEMATIC STUDY OF *ANTENNARIA MEDIA*,  
*A. PULCHELLA*, AND *A. SCABRA*  
(ASTERACEAE: INULEAE) OF THE SIERRA  
NEVADA AND WHITE MOUNTAINS

RANDALL J. BAYER

University of Alberta, Department of Botany,  
Edmonton, Alberta T6G 2E9, Canada

ABSTRACT

*Antennaria pulchella* and *A. media* are a diploid progenitor–polyploid derivative pair of taxa that occur in the cordilleran system of western North America. *Antennaria scabra* is a glandular form of *A. pulchella* and is considered to be part of the variation within that taxon. The sexually reproducing diploid, *A. pulchella*, has a very restricted range, in the subalpine-alpine zones of the southern Sierra Nevada from the area around Lake Tahoe to the Mt. Whitney region. *Antennaria media* is a widespread polyploid that occurs throughout the cordilleran system of western North America from the Mexican border to the subarctic. They are both part of a large arctic/alpine species complex known as *A. alpina*. One of the diploid progenitors of *A. media*, and consequently the *A. alpina* complex, is *A. pulchella*.

*Antennaria media* E. Greene is a widespread polyploid species occurring throughout the alpine zones of most of the western North American mountain ranges from New Mexico and Arizona to southern Yukon. The type of *A. media* is from the high Sierra Nevada above Coldstream, Placer Co., California. Some authors follow the lead of Jepson (1925) and consider *A. media* to be an infraspecific taxon of *A. alpina* (L.) Gaertner, recognizing it as *A. alpina* var. *media* (E. Greene) Jepson. *Antennaria alpina*, in the strict sense, is a widespread circumboreal arctic-subarctic taxon, whereas *A. media* is a North American cordilleran segregate of the *A. alpina* complex (Bayer 1987, 1989B). *Antennaria media* is composed primarily of tetraploids ( $2n=56$ ), but higher ploidy levels up to octoploid ( $2n=112$ ) are frequently encountered (Bayer and Stebbins 1987; Bayer 1987) especially in the Rocky Mountains and other areas of its range away from the Sierra Nevada and Cascade Range. Staminate and pistillate plants occur in approximately equal frequencies in populations of *A. media* from the Sierra Nevada and Cascade Range, but in other parts of its range populations tend to be composed entirely of pistillate plants (Bayer and Stebbins pers. field and herbarium specimen obs.).

A series of diminutive herbarium specimens identified as *A. media*, including the type specimen of *A. pulchella* E. Greene from Mt. Goddard in the Sierra Nevada and *A. scabra* E. Greene (= *A. media*



subspecies *ciliata* E. Nelson) from the White Mountains, occur in the southern Sierra Nevada. Two sets of living plants, referable to *A. pulchella*, were collected in 1982 by G. L. Stebbins in the Sierra Nevada of California near Eagle Lake, Tulare Co. and Brainerd Lake, Inyo Co. These plants proved to have  $2n=28$  (Bayer 1984), indicating the fact that *A. pulchella* is a diploid. Studies of isozymes have established that diploid *A. pulchella* is fixed for one allele at the *Tpi-1* locus, but the polyploid plants of *A. media* are often fixed for an alternative allele not encountered in the diploids (Bayer 1989a). So although *A. pulchella* is probably one of the diploid progenitors of the *A. media* polyploids, they are probably not strict autopolyploid derivatives of *A. pulchella*, but instead of hybrid polyploid origin (Bayer 1989a). *Antennaria scabra* is often recognized as *A. alpina* var. *scabra* (E. Greene) Jepson, but its relationship to *A. media* and *A. pulchella* has been undecided and debatable.

These taxa had previously been treated as a single variable taxon, *A. media* (Bayer 1984; Bayer and Stebbins 1987; Bayer 1988). This circumscription should now be reviewed, especially in light of our recent field work (1987) in the Sierra Nevada with these taxa which yielded additional chromosomal and isozyme divergence data. Several questions need to be addressed. Is diploid *A. pulchella* morphologically distinct from polyploid *A. media* and, if so, what characters can be used most reliably to separate the taxa? What is the relationship of *A. scabra* to both *A. media* and *A. pulchella*? What is the range of the narrow endemics, *A. pulchella* and *A. scabra*, with respect to *A. media*? Morphometric and cytogeographic analyses are used to address these questions. The final outcome is a revised systematic treatment of these taxa.

## METHODS

Herbarium specimens borrowed from ALTA, CAS, DAV, DS, GH, JEPS, NY, RM, UC, and US provided both morphological and distributional data. Chromosome counts were obtained from root-tip squashes using the Feulgen staining reaction outlined in Bayer (1984).

Sixty-one specimens, including approximately equal proportions morphologically referable to *A. media* and *A. pulchella/A. scabra*, were used in the analysis. Type specimens for each of the three names were included among the 61 specimens, as well as several recent personal collections of known chromosome number. Specimens representing the range of morphological variation in all taxa were selected as a means of assuring that a representative sample of the morphological variability within each taxon was being analyzed. Thirty-eight vegetative and morphological characters were measured. The characters used in this study are identical with those listed in Bayer (1989c).



Morphological variation in the taxa was assessed using multivariate morphometric analyses, including principal components analysis (PCA) and cluster analyses. The analyses were implemented through the use of the NTSYS-pc programs (Rohlf 1987). The data were standardized so that each character had a mean of zero and a standard deviation of unity through the use of the STAND subroutine of NTSYS. A similarity matrix of product-moment correlations of the characters and a matrix of average taxonomic distances from the OTU's (Operational Taxonomic Units = specimens) were derived using the SIMINT subroutine. The EIGEN subroutine was used to calculate eigenvalue and eigenvector matrices from the matrix of product-moment correlations. The OTU's were subsequently projected onto axes, the eigenvectors, using the PROJ subroutine, thereby completing the PCA. A 3-dimensional graph of the OTU's on the first three principal components was plotted by the MOD3DG subroutine of NTSYS. A cluster analysis using the unweighted pair-group method (UPGMA) was generated by subjecting the distance matrix produced by SIMINT to analysis by the SAHN subroutine.

## RESULTS

*Morphometrics.* The results of the PCA and cluster analysis (Figs. 1 and 2) indicate that two morphologically distinct groups can be recognized: *A. media* and *A. pulchella-A. scabra*. The cluster analysis, illustrated as a phenogram (Fig. 2), shows a distinct separation of *A. media* from the *A. pulchella* complex. A morphological gap is evident in the PCA between the two groups on the plot of factor 1 vs. factor 2 (Fig. 1), which accounts for 46.4% of the total variation. In both analyses, eight confirmed diploid specimens are grouped within the *A. pulchella* complex, whereas three verified tetraploids are within the *A. media* complex (Figs. 1 and 2). The type specimens of *A. media* and *A. pulchella* are clustered within the other specimens assigned to these taxa, but the type of *A. scabra* is grouped with the *A. pulchella* complex. In PCA, highest loadings for factor 1 were staminate and pistillate corolla length, pollen grain diameter, length of the longest (lowermost) cauline leaf, and height of the staminate involucre. Factor 2 has high loadings for pistillate pappus length, corolla length, achene length, and phyllary color, as well as length of the leaves in the basal rosettes. The two groups, *A. media* and *A. pulchella*, differentiate best along factor 1; consequently, characters having high loadings along this axis were examined as potential "key characters" that could be used confidently to separate the species. Investigation of these characters indicated that pistillate and staminate corolla length and length of the lowermost cauline leaves are the most reliable characters to separate the taxa. A trivariate plot of the OTU's using these three variables (Fig. 3) demonstrates the resolving power of these characters to distinguish the species.



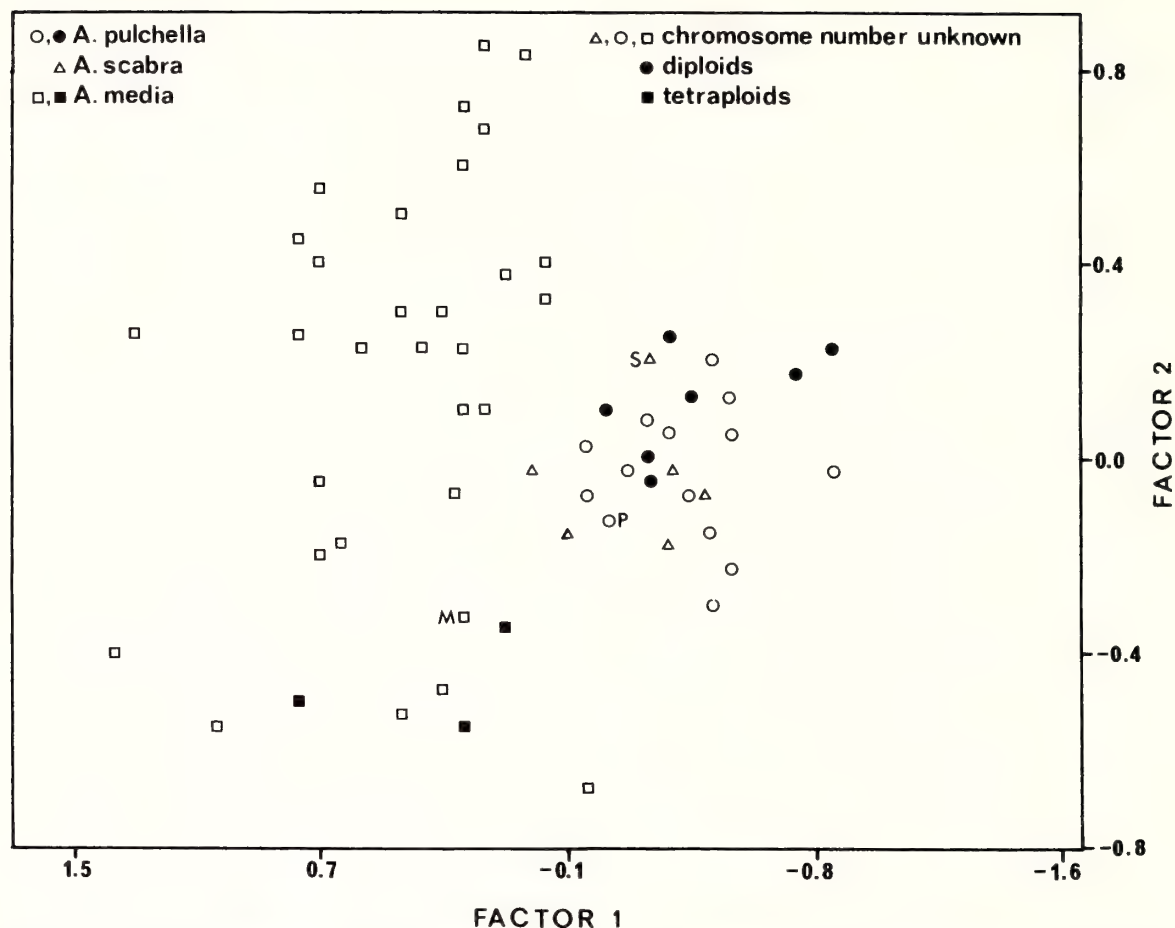


FIG. 1. PCA composed of a total of 61 OTU's (specimens) of *Antennaria media*, *A. pulchella*, and *A. scabra*. Holotypes of *A. media* (US), *A. pulchella* (US) and *A. scabra* (US) are marked with "M", "P", and "S", respectively.

*Cytology and cytogeography.* The results show that *A. pulchella* is diploid from eight localities in the Sierra Nevada of California and Nevada, based on three previously published reports (California, Inyo Co., C-235; Tulare Co., C-245 [Bayer 1984] and Nevada, Washoe Co., C-450 [Bayer and Stebbins 1987]) and five new determinations (California, Inyo Co., CA-700, CA-707, CA-724, CA-732; Mono Co., CA-720 [Voucher specimens are at ALTA and RM.]). Previously published chromosome reports for *A. media* (Bayer and Stebbins 1981; Bayer 1984; Bayer and Stebbins 1987) indicate that the tetraploids are the most widespread and predominant cytotype in the species. Twenty-two chromosome counts of *A. media* from California and Oregon have yielded only tetraploid counts (Bayer and Stebbins 1987).

## DISCUSSION

*Antennaria pulchella* should be recognized as a separate species from *A. media* because it is morphologically distinct from *A. media*. It is also presumably reproductively isolated because it is diploid, whereas *A. media* is tetraploid in the area of sympatry between the two taxa. Some tetraploids have allozymes that have not been de-



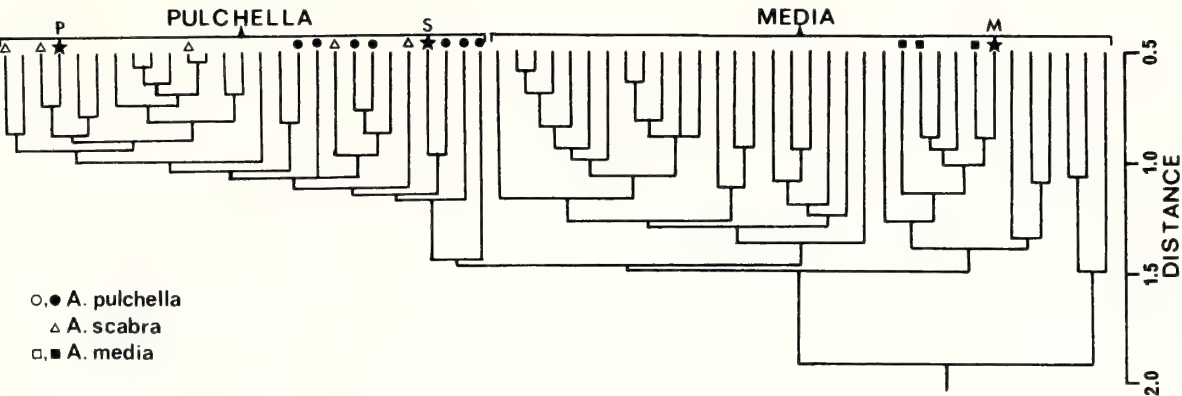


FIG. 2. Distance phenogram representing relationships among 61 OTU's of *Antennaria media*, *A. pulchella*, and *A. scabra*. Unlabeled OTU's belong to the taxon indicated at the top of the bracket that they cluster under. Holotypes of *A. media* (US), *A. pulchella* (US) and *A. scabra* (US) are marked with "M", "P", and "S", respectively.

tected in *A. pulchella* indicating that they are probably not simply autopolyploid derivatives of *A. pulchella* (Bayer 1989a). Also *A. pulchella* frequently possesses various quantities of glandular hairs, whereas *A. media* is usually non-glandular.

*Antennaria scabra* represents a very glandular form of *A. pulchella*. The type of *A. scabra* is included in the *A. pulchella* cluster. Other specimens of the taxon are very similar to typical *A. pulchella*, as indicated by morphometric analyses (Figs. 1 and 2), except they

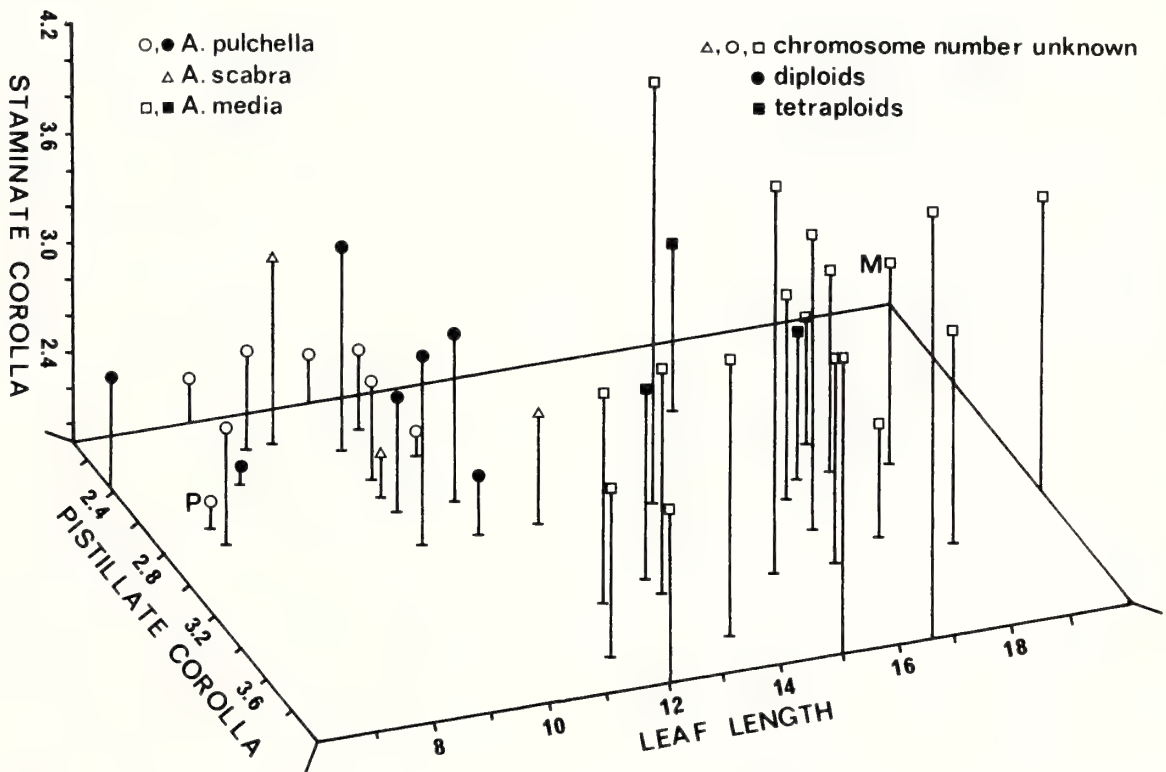


FIG. 3. Trivariate plot of *Antennaria media*, *A. pulchella*, and *A. scabra* specimens. The three axes consist of length of the staminate corolla, length of the pistillate corolla, and length of the lowermost cauline leaf. Holotypes of *A. media* (US) and *A. pulchella* (US) are marked with "M" and "P", respectively.



possess numerous stalked purple glandular hairs and are less pubescent than typical *A. pulchella*.

Two aspects of *A. pulchella* and *A. scabra* provide additional evidence in support of the proposed conspecific relationship. The ranges of both narrowly restricted endemics are completely overlapping (Fig. 4) and congruent, and there are several mixed collections, e.g., *Bayer et al. CA-700* (ALTA), *Bayer et al. CA-724* (ALTA), and *Sharsmith 3029A/3029B* (UC) (representative specimens). Many *A. pulchella* have some glandular hairs on the upper cauline leaves and stem as well as on the involucre. *Bayer et al. CA-700* and *CA-724* contain a relatively small proportion of clones that could be referred to *A. scabra*; most are the *A. pulchella* phenotype with varying degrees of glandulosity. I suggest that glandulosity is a multistate character in *A. pulchella* and that *A. scabra* simply represents one extreme. The character segregates in some populations, therefore the mixed populations of the two morphotypes, *A. pulchella* and *A. scabra*, occur.

Staminate and pistillate corolla length, and length of the longest (lowermost) cauline leaf are the most reliable characters for separating the taxa. They can be used to construct a key to separate *A. media* from *A. pulchella* (sensu lato). Measurements should be made from mature specimens only, usually at anthesis or later. A good indication of maturity of corollas in *Antennaria* is their length when compared to the pappus bristles. At maturity the corolla of both genders almost equals the pappus in length (often about 1 mm shorter than the pappus). The pappus matures more quickly, consequently in immature heads the corollas are much shorter than the pappus bristles. In pistillate corollas, the measurement should be from the top of the ovary (achene) to the tip of the corolla, in staminate corollas from the summit of the rudimentary ovary to the base of the sinus between the perianth lobes. Glandulosity, gender ratio, and geographic distribution can also be used as minor characters to help differentiate the taxa.

#### KEY TO *ANTENNARIA MEDIA* AND *A. PULCHELLA*

- A. Pistillate corolla less than or equal to 3.0 mm at maturity; staminate corolla usually less than or equal to 2.75 mm at anthesis; lowermost cauline leaf less than or equal to 11 mm at maturity; glandular hairs often present on basal leaves, cauline leaves and stem; staminate plants always present in populations; plants of the Sierra Nevada from the Lake Tahoe region south to the Mt. Whitney area, California and adjacent Nevada. . . . . *A. pulchella*
- A'. Pistillate corolla greater than 3.0 mm at maturity; staminate corolla usually greater than 2.75 mm at anthesis; lowermost cauline leaf greater than 11 mm at maturity; glandular hairs absent from leaves, stems and involucres; staminate plants often absent from populations; plants widespread in western North America from California, Arizona, and New Mexico north to Yukon and Northwest Territories. . . . . *A. media*



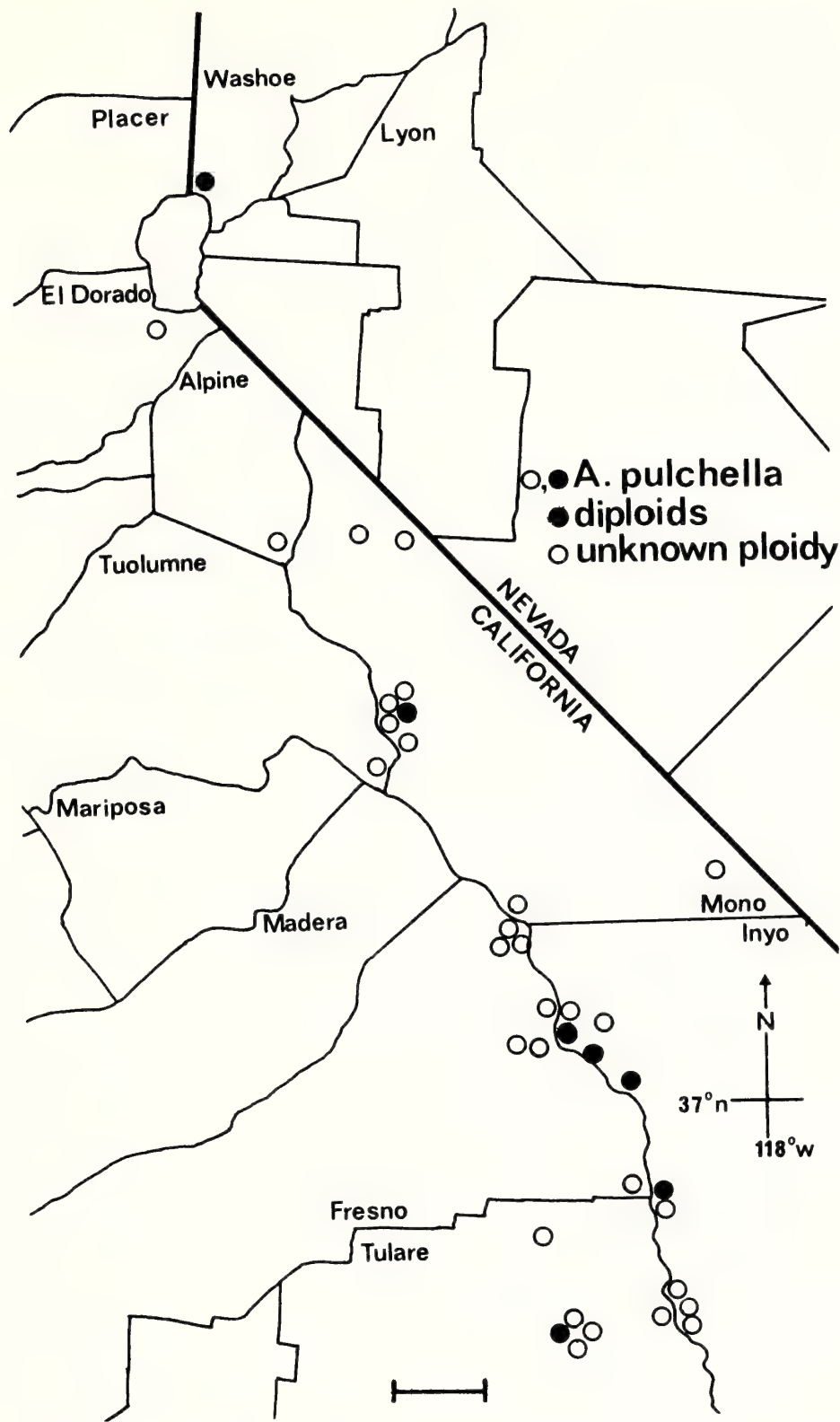


FIG. 4. Distribution of *Antennaria pulchella* (including *A. scabra*) in the Sierra Nevada and White Mountains of California and Nevada. Each symbol depicts one collection. Bar = 25 km.

TAXONOMIC TREATMENT

1. *ANTENNARIA PULCHELLA* E. Greene, Leaflet Bot. Observ. Crit. 2: 149. 1911.—TYPE: USA, California, “Plants of the Sierra Nevada Mtns., Mt. Goddard, alt. 11,000’” (fide label), 24–26 Jul



1900, *H. M. Hall and H. P. Chandler* 686 (holotype, US! #390722).

*Antennaria media* E. Greene subsp. *ciliata* E. Nelson, Proc. U.S. Natl. Mus. 23:700. 1901.—TYPE: USA, California, “White Mts. Mono Co., Calif. 12,000 ft.” (fide label), Jul 1886, *Wm. Shockley* 444 (holotype, US! #47044).—*A. scabra* E. Greene, Leaflet Bot. Observ. Crit. 2:150. 1911.—*A. alpina* var. *scabra* (E. Greene) Jepson, Manual Fl. Pl. Calif. 1070. 1925.—TYPE: USA, California, “White Mts. Mono Co., Calif. 12,000 ft.” (fide label), Jul 1886, *Wm. Shockley* 444 (holotype, US! #47044). The taxon was first described as *A. media* subsp. *ciliata* by E. Nelson (1901), the type being *Shockley* 444. Nelson also mentioned a paratype, *Coville and Funston* 2160, in his protologue. Ten years afterward E. Greene (1911) described *A. scabra*, citing *Shockley* 444 as the type and *Colville and Funston* 2160 as a paratype, but not making any reference to the earlier description of *A. media* subsp. *ciliata* by Nelson. They are nomenclatural synonyms.

Mat-forming perennial herbs, odorless, with 3–6 leafy stolons per basal rosette; rosette-leaves spatulate to linear-cuneate, 5–14 in number, 6–12 mm long, 1.5–4.5 mm wide, usually with distinct petioles 1–3 mm long, glabrescent-scabrous to canescent, often also with purple glandular hairs. Stolons decumbent, 2–4(1–9) cm long, with 9–22 leaves, the proximal leaves 3–8 mm long, 0.5–2 mm wide, the distal leaves 6–12 mm long, 1.5–3.5 mm wide. Flowering stem (1–)3–12 cm high; cauline leaves 4–8(–9), linear, the lower 6–11(–13) mm long, 1–2.5 mm wide, the upper 3–8(–10) mm long, 0.5–1.5 mm wide, only those about the heads sometimes possessing linear-lanceolate, scarious appendages at their tips (flags). Pistillate heads 4–6(3–7), in corymbose clusters; involucre 3.5–4.5(–6) mm high; phyllaries in 2 or 3 series, acute to blunt, scarious, the longest 3.5–4.5(–5) mm long, 0.5–1.2 mm wide, colors various, the tips usually dark-green or black, but often brown, light brown, or white, with base of a darker brown or black. Florets 25–60 per head; corollas 2–3(–3.3) mm long, pappus 3.3–4(–4.5) mm long, achenes 0.7–1.3 mm long, with or without papillae. Staminate plant as frequent as pistillate, staminate heads 3–6, in corymbose clusters; involucre (3–)4–5 mm high; phyllaries 3.5–4.5 mm long; 0.7–2 mm wide, corolla 1.9–2.8(–3) mm long; pappus clavate, 2.5–3.5 mm long, pollen 16–22 micrometers in diameter;  $2n=28$ .

*Distribution and habitat* (Fig. 4). The known range of *A. pulchella* extends from Mt. Rose, Nevada, to Primrose Lake in the southern Sierra Nevada, where it is found primarily on the eastern slope with scattered sites on the western slope. Habitats are subalpine to alpine; 2800 m in the north to 3700 m in the south. One record indicates



2300 m, but may be in error (*McGregor 162*; representative specimens). Sites generally mesic, near the margins of tarns and streams or where there are intermittent streams or run-off from large snow-masses that provide moisture for most of the summer.

*Representative specimens.* USA, California, Alpine Co.: White Mts., 8 Sep 1936, *Albertus 370* (USFS). El Dorado Co.: Desolation Valley, 18 Aug 1909, *McGregor 162* (NY). Fresno Co.: basin just N of Mono Pass, head of Mono Creek, 8 Aug 1937, *Sharsmith 3029A* and *3029B* (NY, UC); Mt. Goddard, 24–26 Jul 1900, *Hall and Chandler 686* (UC); Rae Lakes Basin, Kings Canyon National Park, isthmus between first and second Rae Lakes, 3 Aug 1978, *Burke 669* (DAV); Muir Pass, 11,955 ft, 28 Jul 1952, *Raven 4707* (CAS); slope W of Second Recess, 11,000 ft, 30 Jul 1953, *Raven 5947* (CAS); McGee Lakes to Wanda Lake, 25 Jul 1952, *Raven 4687* (CAS). Inyo Co.: Slim Lake, SE of Kearsarge Pass, W of Independence, 8 Aug 1942, *Alexander and Kellogg 3285* (GH); Cottonwood Lakes, SW of Lone Pine, about rocks, E side from fifth lake, 29 Aug 1942, *Alexander and Kellogg 3407* (NY, UC); Mt. Whitney, Consultation Lake, E slope, 23 Jul 1935, *Rose 35498* (CAS); Big Pine Creek, near Brainerd Lake, 10 Sep 1982, *Vasey C-235* (DAV); Pee-wee-pot-hole, NE of Dingleberry Lake, above Lake Sabrina, 11 Aug 1950, *Raven and Stebbins 295* (UC); Coyote Ridge, Sierra Nevada, 11,700 ft, 7 Aug 1950, *Raven and Stebbins 211* (UC); Inyo National Forest, Trail from Blue Lake to Dingleberry Lake, 16 Jul 1987, *Bayer, DeLuca, and Lebedyk CA-724* (ALTA, CAN, DAV, RM); trail to Matlock Lake, vicinity of Kearsarge Pass, 13 Jul 1987, *Bayer, DeLuca, and Lebedyk CA-707* (ALTA, CAN, DAV, RM); lake basin below Chocolate Mt. and Hurd Pk., steep rocky slope between Mary Louise Lakes and Bull Lake, 16 Jul 1987, *Bayer, DeLuca, and Lebedyk CA-732* (ALTA, CAN, DAV, RM); Sierra Nevada, near first Cottonwood Lake, common among grasses and sedges adjacent to Cottonwood Creek, 12 Jul 1987, *Bayer, DeLuca, and Lebedyk CA-700* (ALTA, CAN, DAV, RM); exposed granite rocks, Piute Pass, 22 Jul 1934, *Ferris 8940* (DS). Mono Co.: Sweetwater Mts., Deep Creek, common among rocks up the stream, 5 Aug 1944, *Alexander and Kellogg 4011* (GH); Yosemite National Park, Mono Pass, 21 Aug 1907, *Eastwood 570* (CAS); H. M. Hall Natural Area, 25 Jul 1954, *Kruckeberg 3576* (NY, RM); Dana Plateau, in gravels of unglaciated granitics, vicinity of Mt. Dana, 13 Jul 1937, *Sharsmith 2433* (UC); mountains above Saddlebag Lake, 14 Aug 1927, *Hastings s.n.* (NY); alpine fell-field at head of Sweetwater Creek, Sweetwater Mts., 24 Jul 1955, *Munz 21220* (NY); vicinity of Tioga Pass, moist drainage area at S end of Saddlebag Lake, 14 Jul 1987, *Bayer, DeLuca, and Lebedyk CA-720* (ALTA, CAN, RM); H. M. Hall Natural Area, 30 Jun 1934, *Blake 11822* (GH). Tulare Co.: Upper Franklin Lake,



Mineral King Game Refuge, Sequoia National Park, 28 Jun 1966, *Rice, Pemble, and Fleschner 187* (DAV); W side of Eagle Lake, above Mineral King, 16 Sep 1982, *Stebbins, Vasey, and Stephens C-245* (DAV); Sequoia National Park, S end of Eagle Lake, 3 mi above Mineral King, (in part) 13 Sep 1932, *Bracelin 726* (GH, NY); S shore of Twin Lakes, Sequoia National Park, 7 Sep 1932, *Bracelin 703* (GH); Primrose Lake, 11,500 ft, 24 Jul 1949, *Howell 25702* (CAS); SE of Farewell Gap, 20 July 1951, *Howell 28008* (CAS). Tuolumne Co., Kuna Crest above Helen Lake, Parker Pass region, 20 Jul 1937, *Sharsmith 2620* (NY). Nevada, Washoe Co., S of the summit of Mt. Rose, along Third Creek, 15 Jul 1984, *Stebbins, Kunz, and Vasey C-450* (DAV).

*Relationships.* *Antennaria pulchella* is perhaps most closely related to *A. corymbosa* E. Nelson, a sexual diploid species of the northern Rockies that has disjunct populations in the Sierra Nevada (Bayer and Stebbins 1987). *Antennaria pulchella* possesses *Tpi-1<sup>b</sup>*, an allele that is shared only with *A. corymbosa* and some tetraploid segregates of *A. media* (Bayer 1989a). Both species occur in mesic habitats at subalpine elevations. Many individuals of *A. pulchella* have linear-oblongate basal leaves and phyllaries that are white tipped with a black base, characteristics that distinguish *A. corymbosa*. *Antennaria pulchella* is also perhaps closely related to arctic *A. monocephala* DC., which occurs in mesic habitats on the margins of solifluction lobes. It differs from *A. pulchella* in its monocephalous flower stalks and glabrous adaxial leaf surfaces. Unfortunately, isozyme variation has not yet been investigated in *A. monocephala*, so it cannot yet be compared to *A. corymbosa* or *A. pulchella*.

2. *Antennaria media* E. Greene, Pittonia 3:286. 1898.—*Antennaria alpina* (L.) Gaertn. var. *media* (E. Greene) Jepson, Manual Fl. Pl. Calif. 1070. 1925.—LECTOTYPE (Nelson 1901, Proc. U.S. Natl. Mus. 23:700.): USA, California, Placer Co., “Mts. above Coldstream” (fide label), 31 Jul 1892, *C. F. Sonne s.n.* (US! #310514).

*Antennaria austromontana* E. Nelson, Proc. U.S. Natl. Mus. 23:703. 1901.—TYPE: USA, Utah, “Marysvale, Utah, Alt. 11,700 ft.” (fide label), 28 Aug 1894, *M. E. Jones 5522* (holotype, US! #326693).

*Antennaria modesta* E. Greene, Ottawa Naturalist 30:72. 1906.—LECTOTYPE (Bayer 1988, Taxon 37:292–298.): CANADA, British Columbia, “Second summit W of Skagit River, B.C. alt. 6,000 ft.” (fide label), 29 Jul 1905, *J. M. Macoun Canad. Geo. Survey #69,334* (NDG; Type description reads “25” July not “29” July).

*Antennaria densa* E. Greene, Leaf. Bot. Observ. Crit. 2:151. 1911.—TYPE (Bayer 1988, Taxon 37:292–298.): USA, California, “Mt.



San Gorgonio, San Bernardino mountains, altitude 11,000 ft.” (fide label), 12 Jul 1908, *L. Abrams and E. A. McGregor 751* (lectotype, US! #613419).

*Antennaria candida* E. Greene, Leaf. Bot. Observ. Crit. 2:151. 1911.—TYPE: USA, California, “Mt. Rainier, alt. 9,000 ft.” (fide label), 14 Aug 1895, *O. D. Allen 141* (holotype, US! #314044).

Mat-forming perennial herbs, odorless, with 3–6 leafy stolons per basal rosette; rosette-leaves spatulate to linear-cuneate, 5–11 in number, (6–)9–19 mm long, 2.5–6 mm wide, usually with distinct petioles 1–5 mm long, canescent and usually non-glandular. Stolons decumbent, 1–4 cm long, with 7–20 leaves, the proximal leaves 3–10(–14) mm long, 0.5–3 mm wide, the distal leaves 6–19 mm long, 1.5–5.5 mm wide. Flowering stem (2–)5–13 cm high; cauline leaves 4–10, linear, the lower (9–)11–20 mm long, 1.5–4 mm wide, the upper 5–11 mm long, 0.5–2 mm wide, only those about the heads infrequently possessing subulate, scarious appendages at their tips (flags). Pistillate heads 4–7(2–9), in corymbose clusters and sometimes with elongate pedicels; involucre (4–)5–8 mm high; phyllaries in 2 or 3 series, acute to blunt, scarious, the longest (3.5–)4–6.5 mm long, 0.7–1.6 mm wide, colors various, the tips usually dark-green or black, but much less often brown, light brown, or white, with base of a darker brown or black. Florets 35–80 per head; corollas (2.5–)3–4.5 mm long, pappus (3.5–)4–5.5 mm long, achenes 0.6–1.6 mm long, with or without papillae. Staminate plant as often as frequent as pistillate, but often completely lacking from populations, staminate heads 3–7, in corymbose clusters; involucre (3.5–)4.5–6.5 mm high; phyllaries (3.5–)4–6 mm long; 0.7–2 mm wide, corolla (2.5–)2.8–4.5 mm long; pappus clavate, 2.5–4.5 mm long, pollen 19–25 micrometers in diameter;  $2n=56, 98, 112$ .

*Distribution and habitat.* *Antennaria media* occurs in subalpine to alpine/arctic tundra zones from New Mexico and Arizona into the North American subarctic. In California, it occurs at elevations and in habitats that are similar to those of *A. pulchella*. A detailed distribution map of *A. media* must wait until its status in the northern portions of its range can be investigated more closely.

*Representative specimens.* CANADA, Alberta, Waterton Lakes National Park, alpine summit of Mt. Crandell, 9 Aug 1953, *Breitung 17368* (ALTA); Jasper National Park, Sunwapta Pass, shoulder of Wilcox Mtn., 13 Jul 1939, *Moss 4974* (ALTA); Jasper National Park, along Tonquin Valley trail, switchback area, 19 Jul 1971, *Scotter 16858* (ALTA). British Columbia, hillside, road from Anahim Lake to Bella Colla, 8 Jul 1956, *Calder, Parmelee, and Taylor 18518* (DAO); Mt. McLean at Lillooet, shale flat, 6 Sep 1954, *Calder, Savile, and Ferguson 15510* (DAO); on coarse talus at treeline on E slope of Starvation Peak, 29 Jul 1958, *Taylor, Calder, and Ferguson 3206*



(DAO). Vancouver Island, trail to summit of Mt. Albert Edward, Forbidden Plateau, 6 Aug 1961, *Calder and MacKay 32168* (DAO); Vancouver Island, Mt. Arrowsmith near Alberni, 26–27 Jul 1956, *Calder, Parmelee, and Taylor 19451* (DAO). USA, California, Inyo Co.: on trail from North Lake to Piute Pass, 9 Sep 1982, *Stebbins and Vasey C-232* (DAV). Mono Co.: White Mts., above McAfee Meadows, 6 Aug 1945, *Maguire and Holmgren 28086* (NY). Tulare Co.: S Margin of southwest lake, Maggie Lakes, 14 Sep 1982, *Stebbins, Vasey, and Stephens C-243* (DAV); N end of Eagle Lake, above Mineral King, 16 Sep 1982, *Stebbins, Vasey, and Stephens C-246* (DAV). Colorado, Grand Co.: ski slopes E of Berthoud Pass, summit of peak near microwave tower, 4 Aug 1984, *Bayer, Dunford, Soreng, and Stebbins CO-468* (RM). Gunnison Co.: alpine peaks and slopes just S of Cottonwood Pass, 20 Jul 1985, *Bayer and Lebedyk CO-520* (RM); alpine summit E side of Cumberland Pass, 1 Aug 1984, *Bayer, Dunford, Soreng, and Stebbins CO-442* (RM). Idaho, Custer Co.: alpine summit of Twin Peaks near fire lookout tower, 31 Jul 1986, *Bayer, Lebedyk, and Joncas ID-604* (CAN, DAO, DAV, RM). Montana, Deerlodge Co.: alpine tundra at Storm Lake Creek Pass (Goat Pass), 26 Jul 1987, *Bayer, DeLuca, and Lebedyk MT-722* (ALTA, CAN, RM). Gallatin Co., E slopes and summit of Mt. Sacajawea, 6 Aug 1986, *Bayer, Lebedyk, and Joncas MT-629* (ALTA, CAN, DAO, RM). Nevada, Nye Co.: Toiyabe Range, in open aspen, head of North Twin River, 27 Jul 1945, *Maguire and Holmgren 25993* (GH). Oregon, Deschutes Co.: N side of Bachelor Butte, 26 Aug 1984, *Stebbins OR-450* (DAV); base of Middle Sister below Renfrew Glacier, 25 Aug 1984, *Stebbins OR-436* (DAV); Three Sisters Wilderness, along trail at Obsidian Falls, 25 Aug 1984, *Stebbins OR-416* (DAV). Utah, Salt Lake Co.: Alta, slopes below Mt. Tuscarora, 24 Jul 1986, *Bayer, Lebedyk, and Joncas UT-604* (RM). Summit Co.: Uinta Mts., S slope of Bald Mtn., 26 Jul 1986, *Bayer, Lebedyk, and Joncas UT-616* (CAN, DAO, RM). Wyoming, Big Horn Co.: Cloud Peak Wilderness, along middle Tensleep Creek near Mirror Lake, 11 Aug 1986, *Bayer, Lebedyk, and Joncas WY-636* (DAV, RM). Fremont Co.: Wind River Range, alpine slopes of Cony Mt., 22 Jul 1985, *Bayer and Lebedyk WY-503* (RM). Park Co.: Hoodoo Basin trail, about 5–6 air mi NW of Stinkingwater Peak, 22 Jul 1985, *Hartman and Nelson 21306* (RM).

#### ACKNOWLEDGMENTS

Support for this research was granted by the Natural Sciences and Engineering Research Council of Canada (NSERC grant #A3797) and by a University of Alberta Central Research Fund Grant (#55-47930). I thank Rob DeLuca, Dan Lebedyk, and Ledyard Stebbins for accompanying me in the field on various occasions and the curators of CAS, DAV, DS, GH, JEPS, NY, RM, UC, and US for the loan of specimens. I am grateful to Jim Morefield, Brett Purdy, Ledyard Stebbins, and John Strother for their helpful comments on earlier versions of this paper.



## LITERATURE CITED

- BAYER, R. J. 1984. Chromosome numbers and taxonomic notes for North American species of *Antennaria* (Asteraceae: Inuleae). *Syst. Bot.* 9:74–83.
- . 1987. Evolution and phylogenetic relationships of the *Antennaria* (Asteraceae: Inuleae) polyploid agamic complexes. *Biol. Zentralbl.* 106(6):683–698.
- . 1988. Typification of western North American *Antennaria* Gaertner (Asteraceae: Inuleae). I. Sexual species of sections *Alpinae*, *Dioicae*, and *Plantaginifoliae*. *Taxon* 37:292–298.
- . 1989a. Patterns of isozyme variation in western North American *Antennaria* (Asteraceae: Inuleae). I. Diploid and polyploid species of section *Alpinae*. *Amer. J. Bot.* 76:679–691.
- . 1989b. A taxonomic revision of the *Antennaria rosea* (Asteraceae: Inuleae: Gnaphaliinae) polyploid complex. *Brittonia* 41:53–60.
- . 1989c. The systematic and phytogeographic study of *Antennaria aromatica* and *A. densifolia* (Asteraceae: Inuleae) in the western North American cordillera. *Madroño* 36:248–259.
- and G. L. STEBBINS. 1981. Chromosome numbers of North American species of *Antennaria* Gaertner (Asteraceae: Inuleae). *Amer. J. Bot.* 68:1342–1349.
- and ———. 1987. Chromosome numbers, patterns of distribution, and apomixis in *Antennaria* (Asteraceae: Inuleae). *Syst. Bot.* 12:305–319.
- GREENE, E. 1911. Accessions to *Antennaria*. *Leaflet Bot. Observ. Crit.* 2:143–151.
- JEPSON, W. L. 1925. A manual of the flowering plants of California. Associated Students Store, Univ. of California, Berkeley.
- NELSON, E. 1901. A revision of certain species of plants of the genus *Antennaria*. *Proc. U.S. Natl. Mus.* 23:697–713.
- ROHLF, F. J. 1987. NTSYS-pc: numerical taxonomy and multivariate analysis system for the IBM PC microcomputer (and compatibles, vers. 1.2). Applied Biol. Statistics, Inc., Setauket, NY.

(Received 18 Sep 1989; revision accepted 4 Jan 1990.)



A NEW SPECIES OF *ERIGERON*  
(ASTERACEAE: ASTEREAEE) FROM COLORADO

STEVE L. O'KANE, JR.

Department of Biology, Box 1137, Washington University,  
St. Louis, MO 63130

ABSTRACT

*Erigeron wilkenii* (section *Spathifolium*), a new species from Dinosaur National Monument in western Colorado, is morphologically similar, and probably related, to *E. tener* A. Gray and *E. cronquistii* Maguire. In regional floras the species might also key to the somewhat similar *E. nematophyllus* or to the distantly related *E. kachinensis* and *E. eatonii*.

Several state records for Colorado (O'Kane, Neely, and Wilken 1988) and the following new species were discovered in 1987 during the first phase of a botanical inventory of Dinosaur National Monument by the Colorado Natural Areas Program (Galatowitsch et al. 1988, unpubl. report, Natl. Park Service, Denver Federal Center).

***Erigeron wilkenii* O'Kane, sp. nov.** (Fig. 1)—TYPE: USA, Colorado, Moffat County: Dinosaur National Monument, near mouth of Pool Canyon in alluvium of the Weber Formation in a *Pinus-Juniperus* community, T6N R104W sect. 12 SE¼, 1713 meters, 1 Jun 1987, S. L. O'Kane, Jr. 3014 (holotype, COLO; isotypes, BRY, RM, NY).

Differt haec species a *E. tener* ligulis albis ventraliter et phyllariis marginibus manifeste scariosis praeditis. Differt haec species a *E. cronquistii* apicibus foliorum mucrone 0.2–0.3 mm longo, nervis et basibus foliorum prominentibus et phyllariis apice non herbaceis.

Delicate erect perennial herb 10–20 cm tall; arising from a short, thin, simple or sparingly branched caudex with crowded internodes; caudex branches sparsely clothed in short, marcescent leaf bases of previous seasons; the root system fine, sparingly branched, mostly approximating a tap root. Stems 1(–4), 0.4–0.5 mm thick, sparsely strigose with mostly appressed and a few ascending Type A (Nesom 1978) trichomes 0.4–0.6 mm long. Leaves entire, basal and cauline; basal leaves tufted in a small rosette, spatulate, 9–62 mm long and 1.1–4.4 mm wide, most tapering in the distal half to a distinct petiole, although a few tapering to near base, sparsely strigose with appressed Type A trichomes up to 0.4 mm long, apex rounded to obtuse, mucronulate, petioles with hairs scattered throughout, not ciliate,



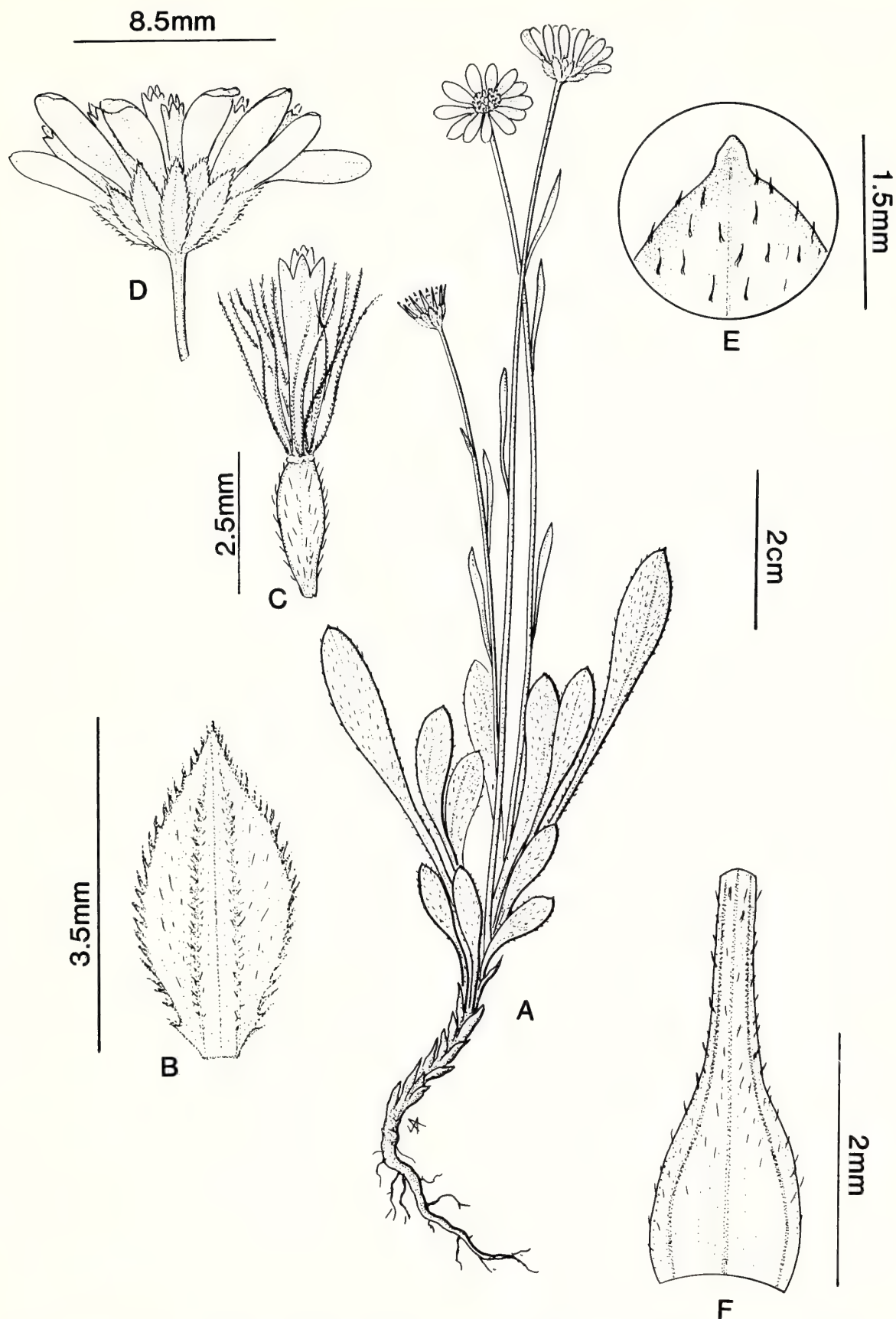


FIG. 1. *Erigeron wilkenii* (drawn from the holotype). A. Habit. B. Inner phyllary, showing wide scarious margins. C. Disc floret. D. Capitulum. E. Mucronulate leaf apex. F. Basal leaf base.



petiole bases enlarged, purplish, membranous, somewhat sheathing and with 3 distinct, slightly raised nerves, not distinctly ciliate but some small hairs like those above sometimes present on margins at very base; cauline leaves linear or linear-oblongate, to 21 mm long and 0.9 mm wide, gradually decreasing in size distally, somewhat more pubescent than basal leaves with similar trichomes and  $\pm$  ciliate, nerves of both basal and cauline leaves indistinct but mid-vein usually evident. Capitula solitary at stem apices, involucre 3.4–4.6 mm high and 6–8.5 mm wide when pressed. Phyllaries 13–20, imbricate in 2–3 series; the inner oblongate, ca. 3.5 mm long and 0.5–1.2 mm wide, scarious except for the narrow central green portion and prominent mid-rib, erose-fimbriate in upper half, apex acute and scarious; the outer lanceolate, somewhat shorter and narrower with less pronounced scarious margins; herbaceous portions of all phyllaries with scattered, short,  $\pm$  crinkly, mostly multicellular Type A hairs and fine, nearly sessile “glandular” Type B trichomes; hairs at base of outer phyllaries more abundant and somewhat longer than those above. Ray flowers (8–)11–12, corollas glabrous, white adaxially, light pink abaxially, 4.4–6.2 mm long, the tube 1.1–1.3 mm long, the lamina 3.2–5.1 mm long and 0.5–1.6 mm wide, lanceolate to oblongate, flat, the apices usually appearing long-acute or acuminate as the distal edges inroll with age or upon drying; disc flowers ca. 15–25, corollas glabrous, yellow, 2.2–3.5 mm long, lobes 0.4–0.6 mm long; style branches 0.6–0.7 mm long including the acute, linear-lanceolate to narrowly deltoid appendages. Pappus of ray and disc flowers shorter than the corollas, 1.5–2.4 mm long, tawny, of (12–)20–30 (averaging 23), fragile, barbellate capillary bristles; shorter setae or squamellae absent, but fractured bristles of dry material may appear as such. Mature achenes not seen, but immature disc and ray achenes essentially alike, 2-nerved, very short pubescent.

*Distribution and habitat.* The only known population of *Erigeron wilkenii* occurs on the sloping, west-facing base of the sheer walls of Pool Canyon above Echo Park. Soils are derived from sandstone of the Weber Formation and are composed of sandy alluvium deposited by intermittent Pool Creek and colluvium from the cliffs above. The site is partially shaded by short-statured trees of *Pinus edulis* Engelm. and *Juniperus osteosperma* (Torrey) Little. *Erigeron wilkenii* grows in accumulated duff and often in mats of *Selaginella densa* Rydb. *Poa fendleriana* (Steudel) Vasey is a common associate. *Pseudotsuga menziesii* (Mirbel) Franco, infrequent in the xeric environment of Dinosaur National Monument, grows above in shaded cracks of the canyon walls. Continuous potential habitat extends the 2.5 km from the type locality into Utah, where *E. wilkenii* can be expected.



TABLE 1. A DIAGNOSTIC COMPARISON OF *ERIGERON WILKENII*, *E. TENER*, *E. CRONQUISTII*, AND *E. NEMATOPHYLLUS*.

| Character         | <i>E. wilkenii</i>   | <i>E. tener</i>  | <i>E. cronquistii</i>  | <i>E. nematophyllus</i>   |
|-------------------|--|--|--|---|
| Ray flower color  | White ventrally, pink dorsally   | Blue or purple   | White or pinkish   | White or pink   |
| Pappus            | Very fragile, shorter than disc corollas   | Not fragile, equaling disc corollas  | Fragile, shorter than disc corollas  | Not fragile, shorter than but sometimes subequal to disc corollas   |
| Inner phyllaries  | Not or barely herbaceous to scarious tip; margins wide, prominently scarious, erose-fimbriulate; not purple-tipped | Herbaceous to tip or nearly so; margins narrow, scarious, sometimes erose-fimbriulate; often purple-tipped | Herbaceous to tip at least toward the midrib; margins prominently scarious, erosulate; purple at tip or throughout | Herbaceous to tip; margins narrow, scarious; often purple-tipped and usu. $\pm$ ciliate at least at the tip |
| Basal leaves      | 9–62 mm long, spatulate  | 13–75 mm long, oblanceolate, elliptic, rhombic or obovate  | 10–44 mm long, oblanceolate to elliptic  | 20–80 mm long, linear or narrowly linear-oblanceolate, rarely narrowly oblanceolate                         |
| Basal leaf apices | Rounded to obtuse, mucronulate   | Acute, some with tip slightly indurated, not or seldom barely mucronulate                                  | Rounded to obtuse, not or rarely barely mucronulate  | Acute, some with tip slightly indurated but not mucronulate   |
| Petioles          | Not distinctly ciliate; sparsely strigillose   | Not or rarely ciliate at very base; strigose, often densely so   | May or may not be ciliate; sparsely strigillose  | Distinctly ciliate toward base; sparsely strigillose but usu. glabrous dorsally                             |
| Petiole bases     | Distinctly 3-nerved  | Nerves not or barely visible, never prominent  | Nerves sometimes visible but never prominent   | Distinctly 3-nerved, lateral 2 sometimes faint  |
| Caudex            | Not or little branched, finely sparsely and shortly clothed with old leaf bases                                    | Moderately branched, mod. stout, mod. clothed with old leaf bases  | Not or more commonly moderately branched, mod. delicate, mod. to densely clothed with old leaf bases               | Usu. much branched, relatively stout, densely clothed with old leaf bases                                   |
| Habit             | Stems one or few   | Stems several to many, caespitose  | Stems several, or rarely one, caespitose   | Stems usu. many, caespitose   |
| Distribution      | Limited to near Echo Park, Moffat Co., CO  | NE and EC CA; NW AZ; S ID; NV; SC OR; W UT; WC and SW WY; not known from CO                                | Limited to the Bear River Mountains, Cache Co., UT   | NW, NC, and SC CO; NE UT; C and SC WY   |



*Relationships and morphology.* Morphologically this species is most closely related to *Erigeron tener* A. Gray and *E. cronquistii* Maguire, taxa thought to be near relatives (Cronquist 1947; Maguire 1944). Like other taxa of the recently described section *Spathifolium* (Nesom 1989), *E. wilkenii* is a small perennial with oblanceolate-spatulate leaves, a strigulose indument of white, short, stiff and sharp-pointed hairs, erect buds, and ligules that neither coil nor reflex. Cronquist's (1947) section *Erigeron* ("Euerigeron") is now subdivided into eight sections (Nesom 1989), including section *Spathifolium*. *Erigeron wilkenii*, like *E. cronquistii* and several other recently described taxa, is another example of a narrow endemic related to *E. tener* that exists outside of the range of that species (Table 1) (Cronquist 1947; Spellenberg and Knight 1989; Nesom 1978; Nesom and Roth 1981). These three taxa are closely allied morphologically but can be distinguished by the combinations of characteristics given in Table 1.

After studying recent collections of related and similar species, I conclude that Cronquist's circumscription of *E. nematophyllus* Rydb. (Cronquist 1947) should be amended to include material possessing basal leaves wide than "linear or linear-oblanceolate" clearly belonging to that species. This material (e.g., *Dorn 3870* [RM, NY], *Neese and Henderson 14198* [BRY, NY, RM], and *O'Kane 2946* [RM]) indicates a closer link, based on leaf characteristics, between Cronquist's "Group VIII", which contains *E. nematophyllus*, and "Group IX" which contains *E. tener* and *E. cronquistii*. In terms of Nesom's (1989) infrageneric classification, this indicates that section *Spathifolium* is related to section *Wyomingia*. In regional floras (e.g., Weber 1987; Welsh et al. 1987), *Erigeron wilkenii* might also key to, in addition to the above, the unrelated *E. kachinensis*, which differs in its much wider leaves, flexuose stems, caudex not clothed with marcescent leaf bases, and habitat of alcove seeps in sandstone canyons. In Dorn (1988), *E. wilkenii* keys with difficulty to *E. tener*, *E. nematophyllus*, or *E. eatonii*. The species is clearly different from *E. eatonii* A. Gray, most notably in its white or pinkish rather than blue ligulate flowers.

High pollen stainability suggests that *E. wilkenii* is neither a recent hybrid nor a racial variant of another species caused by agamospermy with accompanying pollen infertility. Mature anthers from several individuals at or just prior to dehiscence were squashed, stained with Alexander's Stain (Alexander 1969) for 3.5 hours, and then gently flamed. Pollen stainability was 98.9 percent ( $n = 2000$ ; stainable = 1978; inviable = 22).

*Erigeron wilkenii* is named for Dieter H. Wilken, who has, for well over a decade, been an advocate of botanical exploration and rare species conservation in Colorado.



## ACKNOWLEDGMENTS

I thank Steve Petersburg of Dinosaur National Monument for encouraging botanical exploration in the Monument, Betsy Neely for her invaluable assistance during Monument field work, and Dieter Wilken for his aid in this and many other floristic inventories. The curators of BRY, CS, MO, NY, RM, and UTC graciously provided comparative material. John Myers supplied the illustration. G. L. Nesom, R. Spellenberg, and J. L. Strother thoughtfully reviewed the manuscript. S. L. Welsh compared the type collection to similar material from Utah. Field work was supported by the National Park Service through a contract with the Colorado Department of Natural Resources, Colorado Natural Areas Program.

## LITERATURE CITED

- ALEXANDER, M. P. 1969. Differential staining of aborted and nonaborted pollen. *Stain Technol.* 44:117–122.
- CRONQUIST, A. 1947. Revision of the North American species of *Erigeron*, north of Mexico. *Brittonia* 6:121–302.
- DORN, R. D. 1988. Vascular plants of Wyoming. Mountain West Publ., Cheyenne, WY.
- MAGUIRE, B. 1944. Great Basin plants—VIII. New species in *Carex* and *Erigeron*. *Brittonia* 5:199–202.
- NESOM, G. L. 1978. *Erigeron hessii* sp. nov. and *Erigeron kuschei* Eastwood (Compositae), two closely related narrow endemics from the southwestern United States. *Brittonia* 30:440–446.
- . 1989. Infrageneric taxonomy of New World *Erigeron* (Compositae: Asteraceae). *Phytologia* 67:67–93.
- and V. D. ROTH. 1981. *Erigeron scopulinus* (Compositae), an endemic from the southwestern United States. *J. Arizona–Nevada Acad. Sci.* 16:39–42.
- O'KANE, S. L., JR., E. E. NEELY, and D. H. WILKEN. 1988. Noteworthy collections: Colorado. *Madroño* 335:353–354.
- SPELLENBERG, R. and P. KNIGHT. 1989. A new species of *Erigeron* (Asteraceae: Astereae) from central New Mexico. *Madroño* 36:115–121.
- WEBER, W. A. 1987. Colorado flora: western slope. Colorado Associated University Press, Boulder.
- WELSH, S. L., N. D. ATWOOD, L. C. HIGGINS, and S. GOODRICH. 1987. A Utah flora. *Great Basin Naturalist Mem.* 9:1–894.

(Received 16 Jan 1990; revision accepted 9 Apr 1990.)



*POTENTILLA CRISTAE* (ROSACEAE), A NEW SPECIES  
FROM NORTHWESTERN CALIFORNIA

WILLIAM J. FERLATTE

Siskiyou County Department of Agriculture,  
525 South Foothill Drive, Yreka, CA 96097

JOHN L. STROTHER

Herbarium, University of California,  
Berkeley, CA 94720

ABSTRACT

*Potentilla cristae* is known only from Cory Peak, Mt. Eddy, and Marble Mountains in the Klamath Region of northwestern California. It has been confused with *P. flabellifolia*; it is apparently related to *P. brevifolia*.

Our *Potentilla cristae* joins an old and still growing list of Klamath Region endemics (cf. Stebbins and Major 1965). According to Gilbert Muth (pers. comm., unpubl. floristic list for Boulder Peak and adjacent areas) and Jennifer Whipple and Edward Cope (unpubl. ecological survey for a proposed Mt. Eddy research natural area, on file at HSC), at least four other Klamath Region endemics that are also apparently restricted to basic or ultrabasic substrates have ranges that overlap that of *P. cristae* at Cory Peak (CP), Mt. Eddy (ME), and/or Marble Mountains (MM): *Epilobium siskiyouensis* (CP, ME, MM), *Veronica copelandii* (CP, ME, MM), *Eriogonum alpinum* (CP, ME), and *Eriogonum siskiyouense* (CP, ME).

***Potentilla cristae*** Ferlatte & Strother, sp. nov. (Fig. 1).—TYPE: California, Siskiyou Co., China Mt. SE, 7.5' Quad., T40N, R6W, sect. 18, 41°19'34"N, 122°35'56"W, on divide between Scott River and Trinity River drainages, ca. 13 mi SW of Weed, narrow depression on ridge east of Cory Peak, in rocky swale just E of small pond, ca. 2300 m (7500 ft), ultrabasic substrate, 10 Aug 1988, *W. J. Ferlatte 2116* (holotype, UC).

A *P. brevifolio* foliis trifoliolatis, indumentis stipitato-glandulosis et hirsutis, piliis nonglandulosis grossis 1–3 mm longis, et acheniis cristatis alis subcircumnexis 0.05–0.1 mm latis differt.

Caespitose, often mat-forming, perennials from branched root-crowns surmounting an elongate taproot. Leaves, flowering stems, pedicels, and calyces, including bractlets, minutely stipitate-glandular and thinly hirsute with rather coarse, unicellular hairs 1–3 mm



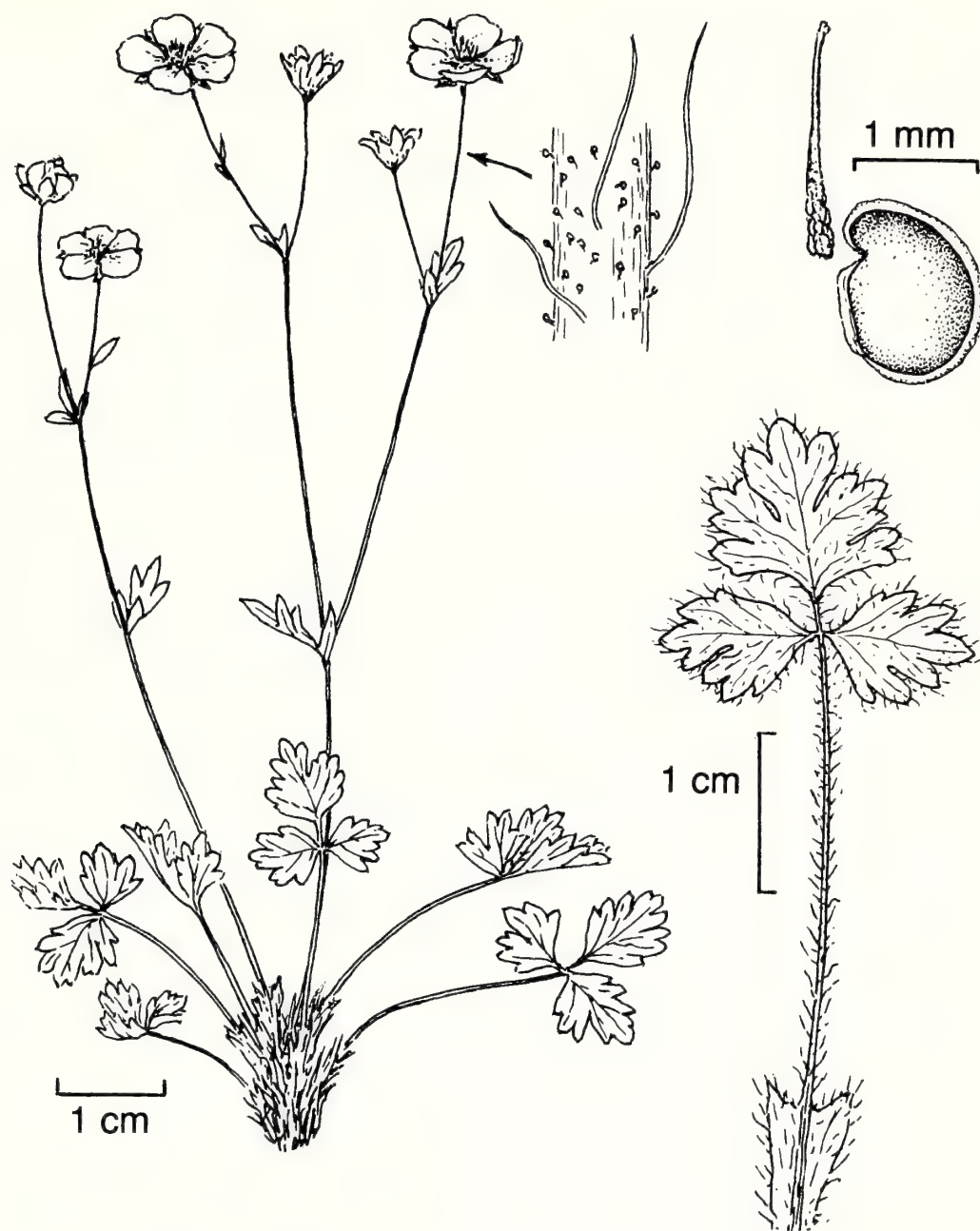


FIG. 1. *Potentilla cristae*. Habit, basal leaf, and achene.

long, these concentrated on margins and abaxial veins, more scattered on adaxial surfaces. Stipules lance-ovate to ovate, 3–5(–12+) mm long, adnate to base of petiole; leaves trifoliate on petioles 1–3+ cm long; leaflets flabellate, deeply 3–5-lobed and coarsely toothed, 5–11 mm long, the laminae typically somewhat coriaceous and more cupped than plane. Flowering stems slender, reddish, 3–10(–15+) cm long, bearing reduced, foliaceous bracts. Flowers 1–4+ per cyme; hypanthium shallow, 3–6+ mm diam.; sepals lance-ovate, 3–5 mm long, alternating bractlets broadly ovate, 2–4 mm long; petals bright yellow, broadly ovate to rounded-rhombic, 3–4 mm long, cuneate at base, scarcely clawed, slightly emarginate; stamens ca. 20, filaments 0.7–1.7 mm long, anthers ca. 0.5 mm long and wide, pollen



grains tetrahedral, 29(27–31)  $\mu\text{m}$  in diam., stainability ca. 100 % ( $n = 100$ ) in lactophenol cotton-blue; receptacles convex becoming conic, to ca. 2 mm high in fruit, hirsute with white hairs to 1.5 mm long; pistils 25–30, ovaries attached laterally ca.  $\frac{1}{3}$  from base, styles stoutish, ca. 1.8–2 mm long, inserted laterally, dilated and glandular at base; achenes brown, laterally compressed, reniform in outline, 1–1.2+ mm long, cristate, ca.  $\frac{3}{4}$  of the circumference bearing a conspicuous (under a lens) wing 0.05–0.1 mm wide, the surface minutely foveolate (at ca.  $20\times$ ) and obscurely rugulose. Chromosome number:  $2n=42$ .

PARATYPES: All California. Siskiyou Co.: China Mt. SE, 7.5' Quad., T40N, R6W, sect. 18, N-facing slope E of Cory Peak, above headwaters of Cabin Meadow Creek, ca. 2200 m (7200 ft), open rocky slope, ultrabasic substrate, 10 Aug 1988, *W. J. Ferlatte 2115* (RSA, UC); same site as 2115, 5 Aug 1989, *Ferlatte 2120* (UC); China Mt. Quad., T40N, R6W, sect. 18, ridge E of Cory Peak, in rocky swale just E of small pond, ca. 2300 m (7500 ft), ultrabasic substrate with *Carex microptera*, *Juncus mertensianus*, 10 Aug 1988, *W. J. Ferlatte 2117* (UC); same site as 2117, 5 Aug 1989, *W. J. Ferlatte 2122* (UC; voucher for chromosome count,  $2n=21_{II}$ ); rocky fell-field of summit region of Mt. Eddy, ca. 2750 m (9000 ft), 13 Aug 1967, *L. R. Heckard 1702* (JEPS); wet gravel on the slope above the head of Wagon Creek on Mt. Eddy in the Hudsonian Zone at ca. 2560 m (about 8400 ft), 3 Jul 1922, *A. A. Heller 13678* (DS); Mt. Eddy, Dobkins Lake, ca. 1825 m (6000 ft), 11 Jun 1934, *D. H. Johnson s.n.* (UC); near summit of Cory Peak, China Mt. Quad., T40N, R6W, sect. 18, ca. 2150 m (7000 ft), on seasonally moist ultrabasic gravels, 3 Aug 1987, *M. A. Knight 951* (UC); scattered on dry limestone [?] in sink, NE face of Marble Mountain, T43N, R12W, sect. 15, ca. 2150 m (7000 ft), 4 Sep 1966, *J. Major et al. s.n.* (DAV); ridge W of Boulder Peak [ca.  $41^{\circ}30'N$ ,  $123^{\circ}W$ ], ca. 2225 m (7600 ft), 10 Aug 1969, *G. J. Muth 1319* (CAS, KNFY). Trinity Co.: progeny of *R. Raiche* and *K. Zadnik 70714* (UC; from near Siskiyou Co. line, Mt. Eddy, near crest of N-facing cirque above Deadfall Lakes, ca. 2400 m (7880 ft), serpentine talus and fell-field slopes where snow banks linger longest, 1 Sep 1987) grown in Univ. Calif. Bot. Gard. (accession number 87.1588), pressed 11 Jul 1988 (UC; voucher for chromosome count,  $2n=21_{II}$ ).

We suggest crested potentilla as an appropriate common name for this species, in reference to the crests or narrow wings that nearly surround the achenes. We also point out that the epithet *cristae* refers both to the morphology of the achenes and to the association of the taxon with the Pacific Crest Trail.

*Potentilla cristae* is known only from the Klamath Region of northern California: on Cory Peak and Mt. Eddy on the boundary between



TABLE 1. COMPARISON OF *POTENTILLA CRISTAE* WITH *P. BREVIFOLIA*, *P. FLABELLIFOLIA*, AND *P. NORVEGICA* SUBSP. *MONSPELIENSIS*.

| Character           | <i>P. cristae</i>                       | <i>P. brevifolia</i>                          | <i>P. flabellifolia</i>                   | <i>P. norvegica</i>              |
|---------------------|---|---|---|----------------------------------|
| Leaf form           | Trifoliolate                            | Pinnate                                       | Trifoliolate                              | Trifoliolate                     |
| Indument            |   |   |   |                                  |
| Stipitate-glandular | Yes                                     | Yes   | Little, if at all                         | No                               |
| Other hairs (mm)    | Coarse, 1–3                             | Fine, 1–2                                     | Fine, 0.5–1                               | Coarse, 1–2.5                    |
| Petal length (mm)   | Mostly 3–4                              | Mostly 4–5                                    | Mostly 6–10                               | Mostly 3–4                       |
| Styles              | Stoutish, dilated and glandular at base | Slender, weakly, if at all, glandular at base | Slender, not dilated or glandular at base | Stout, ± fusiform and glandular  |
| Achenes             | Crested, foveolate, rugulose            | Not crested, smooth, not rugulose             | Not crested, smooth, not rugulose         | Not crested, foveolate, rugulose |

Siskiyou and Trinity counties and from Boulder Peak and Marble Mt. in Siskiyou Co. The sites are all gravelly to cobbly, open slopes or depressions where snow normally lingers into early summer at ca. 1830 to 2750 m. The plants are apparently restricted to basic or ultrabasic substrates. Associated trees found at the type locality included scattered, stunted individuals of *Pinus monticola*, *P. balfouriana*, *P. jeffreyi*, *P. contorta*, and *Abies concolor*; *Potentilla cristae* grew with *Carex microptera*, *Juncus mertensianus*, *Poa pringlei*, *Ivesia gordonii*, *Silene grayi*, *Arenaria nuttallii* subsp. *gregaria*, and *Veronica copelandii*.

In Munz (1959) and Ferlatte (1974), *Potentilla cristae* will key to, or near, *P. flabellifolia*, from which it differs in indument, flower size, and achene morphology (cf. Table 1). In an early draft of a revision of western North American potentillas, Dr. Barbara Ertter (pers. comm.) treated *P. cristae* as near *P. brevifolia*, a species known only from Idaho, Nevada, and Oregon. *Potentilla cristae* and *P. brevifolia* differ most noticeably in leaf morphology, indument, and achene ornamentation (cf. Table 1). In its glandular style bases and weakly developed rugae on the achenes, *P. cristae* is similar to plants that have been called *P. norvegica* subsp. *monspeliensis*. We summarize salient morphological distinctions between *P. cristae* and these taxa in Table 1.

Base chromosome number for *Potentilla* is evidently  $x=7$  and many species have been reported to be polyploid. For two samples of *P. cristae* (see citations of paratypes), we observed  $2n=42$  ( $2n=21_{II}$  at diakinesis and first metaphase of meiosis in pollen parent cells);



the species is apparently hexaploid. Löve (1954) reported  $2n=56$  (i.e., the octaploid level) for *P. norvegica* subsp. *monspeliensis* (as *P. norvegica*). Pojar (1973) reported  $n=14$  (the tetraploid level) for *P. flabellifolia* from British Columbia. We found no report of chromosome number for *P. brevifolia*.

#### ACKNOWLEDGMENTS

We thank staff of Univ. Calif. Bot. Gard. for supplying material for a chromosome count, staff of CAS, DAV, DS, HSC, JEPS, KNFY, POM, RSA, and UC for making specimens available, B. Ertter for considerable help with our study, J. Hickman for bibliographic assistance, M. Knight for a collection from Cory Peak, and A. Smith for help with Latin. The illustration (Fig. 1) was drawn by Emily M. Reid and is used by permission from the Jepson Manual Project.

#### LITERATURE CITED

- FERLATTE, W. J. 1974. A flora of the Trinity Alps of northern California. Univ. California Press, Berkeley.
- LÖVE, A. 1954. Cytotaxonomic remarks on some American species of circumpolar taxa. Svensk Bot. Tidskr. 48:211–232.
- MUNZ, P. A. 1959. A California flora. Univ. California Press, Berkeley.
- POJAR, J. 1973. Levels of polyploidy in four vegetation types in southwestern British Columbia. Canad. J. Bot. 51:621–628.
- STEBBINS, G. L. and J. MAJOR. 1965. Endemism and speciation in the California flora. Ecol. Monogr. 35:1–35.

(Received 8 Dec 1989; revision accepted 9 Apr 1990.)

### ANNOUNCEMENT

#### HESLER VISITING PROFESSORSHIPS IN FLORISTIC BOTANY AT THE UNIVERSITY OF TENNESSEE, KNOXVILLE

A limited number of visiting professorships are available through the L. R. and Esther Hesler Endowment Fund. Proposals are acceptable in all areas of systematic botany with priority given to those which are floristic, revisionary, or monographic in emphasis and deal with the flora of the southern Appalachian Mountains and vicinity in the field or the UTK Herbarium. Applicants should hold faculty (or equivalent) status at a recognized botanical or educational institution. Funding can be used for travel and living expenses and concurrent support from the applicant's institution is strongly recommended. Preliminary correspondence with specific UTK faculty or general inquiries to the Hesler Endowment Fund Committee, Department of Botany, The University of Tennessee, Knoxville, TN 37996-1100 is encouraged.



A NEW VARIETY OF *PENSTEMON FREMONTII*  
(SCROPHULARIACEAE) FROM COLORADO

ROBERT D. DORN  
Box 1471, Cheyenne, WY 82003

ROBERT W. LICHVAR  
RD #2 Keller Road, West Valley, NY 14171

ABSTRACT

*Penstemon fremontii* var. *glabrescens*, a new variety from western Colorado, is described and illustrated. The var. *glabrescens* has glabrous or glabrate leaves and narrow deciduous basal leaves unlike the usually pubescent and mostly persistent basal leaves of var. *fremontii*. Habitats are likewise different and var. *glabrescens* is found only along the southern edge of the range of var. *fremontii*.

While conducting a threatened and endangered species inventory in Garfield County, Colorado, we encountered a *Penstemon* that appeared to be a minor variant of *P. fremontii* Torrey & A. Gray. We later found similar material in the Rocky Mountain Herbarium (RM) from an adjacent county. The habitats were identical and the difference from typical *P. fremontii* was the same.

***Penstemon fremontii* T. & G. var. *glabrescens* Dorn & Lichvar, var. nov. (Fig. 1)—TYPE:** USA, Colorado, Garfield Co.: T7S R100W sect. 24 W $\frac{1}{2}$  NW $\frac{1}{4}$  NW $\frac{1}{4}$ , ca. 30 km SE of Douglas Pass, 2440 m, shale slope in mountain brush, 7 Jul 1987, *Dorn 4656* (holotype, RM; isotypes, to be distributed).

Differt a var. *fremontii* foliis, praeter interdum margines et costam, glabris vel glabratiss.

Perennial from creeping rootstocks. Stems 1.5–3 dm long, short-pubescent to base or nearly so. Leaves opposite, the basal oblanceolate or obovate and sometimes deciduous, transitional to the lanceolate or linear-lanceolate upper leaves, (1–)2–7 cm long, 2–12 mm wide, glabrous, or short-pubescent on midrib and margins, or sometimes the lower blades sparsely pubescent. Inflorescence short-pubescent to glabrate, not glandular. Sepals glabrous, ovate and acuminate, with narrow erose-scarious margins, 3–5 mm long. Corolla blue, 15–22 mm long, the lobes (2–)3–5 mm long, glabrous. Anthers pubescent, 1–1.5 mm long, indehiscent at base, mostly bluish with pale suture margins. Staminode bearded with yellow hairs near tip. Capsules 7–9 mm long.



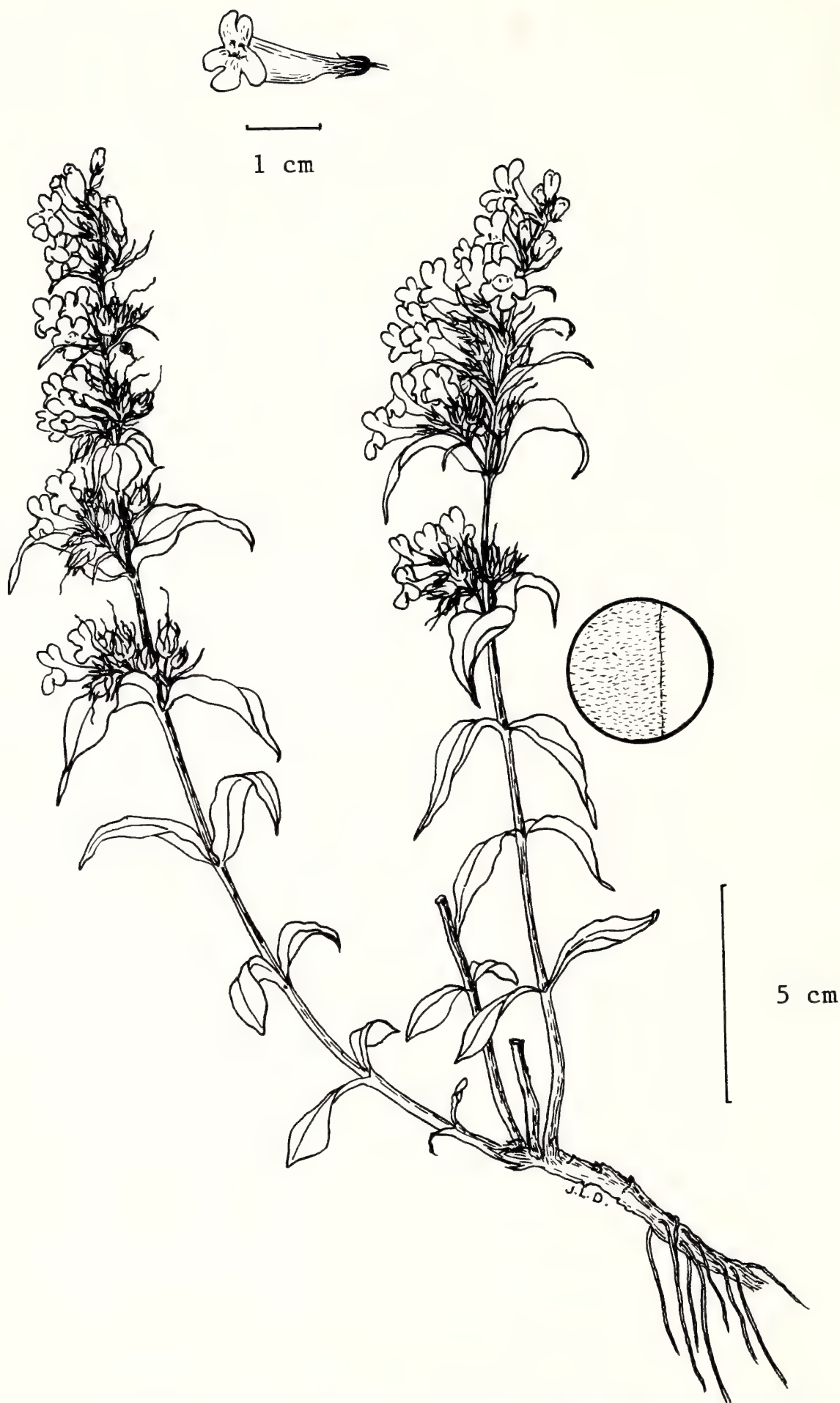


FIG. 1. *Penstemon fremontii* var. *glabrescens*. Circle shows close-up of stem pubescence.



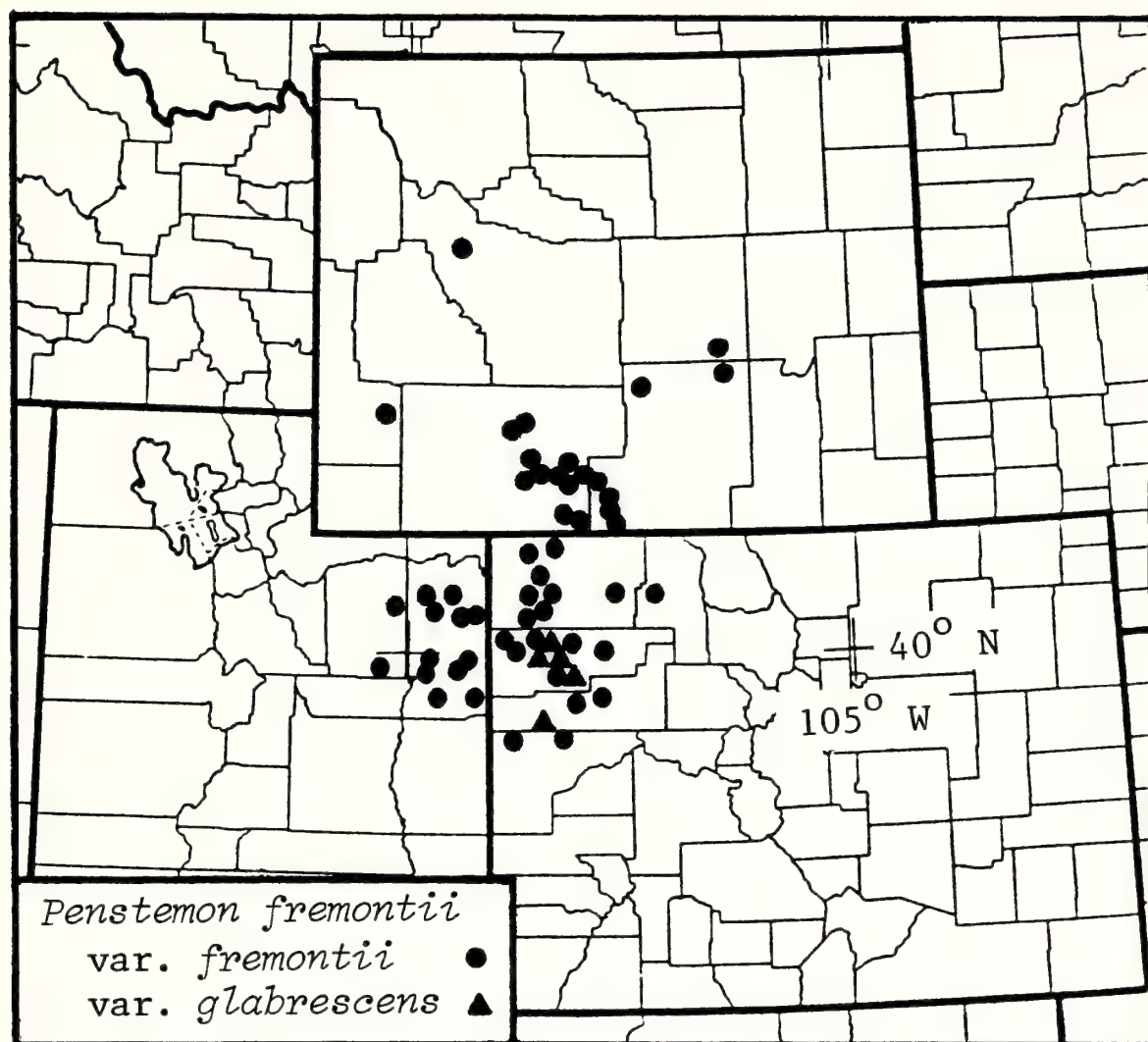


FIG. 2. Colorado, Utah, Wyoming, and parts of adjacent states showing collection locations of *Penstemon fremontii* var. *fremontii* (circles) and var. *glabrescens* (triangles) based on specimens at COLO, CS, and RM. One symbol may represent more than one collection.

PARATYPES: USA, Colorado, Garfield Co.: T8S R99W sect. 6 NE¼ SW¼, 2500 m, shale slope, 8 Jul 1987, *Lichvar* 7339 (RM). Rio Blanco Co.: Fawn Creek Road, Piceance Basin, 1950 m, 6 Jul 1978, *Peterson et al.* 1178b (CS); T2N R98W sect. 17 SE¼ NW¼ NW¼, 1860 m, 10 Jun 1982, *Baker and Nauman* 82-184 (CS); T3S R95W sect. 11 NE¼, 2135 m, 2 Jul 1982, *Kelley and Riefler* 82-37 (CS); along Piceance Ck., 2.1 km N of Rock School, 1885 m, 20 Jun 1983, *Peterson and Rollins* 83-215 (CS, RM); T2S R95W sect. 26 NE¼ SW¼, 2195 m, 3 Jun 1986, *O'Kane* 2408 (COLO, RM); Piceance Creek Valley, 16 km upstream from Rock School, 18 Jun 1988, *Weber* 17922 (COLO).

In var. *fremontii* at least the lower leaves are almost always distinctly short-hairy, but occasional individuals have leaves with a tendency toward glabrescence (e.g., *Neese* 14102 [RM]), the basal leaves tend to be broad and persistent, and the corolla lobes are often short and narrow. In var. *glabrescens* most of the leaves are



TABLE 1. SELECTED CHARACTERISTICS FOR *PENSTEMON FREMONTII* AND RELATED TAXA.

| Species or variety      | Lower stems<br>hairy | Leaf width<br>(mm) | Leaves<br>hairy      | Inflorescence           | Calyx length<br>(mm) | Corolla length<br>(mm) | Anther length<br>(mm) |
|-------------------------|----------------------|--------------------|----------------------|-------------------------|----------------------|------------------------|-----------------------|
| <i>P. fremontii</i>     |                      |                    |                      |                         |                      |                        |                       |
| var. <i>fremontii</i>   | yes                  | 2-18(-27)          | yes                  | pubescent               | 2.5-6.5              | (12-)14-23(-28)        | (1-)1.2-1.5(-1.8)     |
| var. <i>glabrescens</i> | yes                  | 2-12               | midrib and<br>margin | pubescent               | 2-5                  | 14-22                  | 1-1.5                 |
| <i>P. gibbensii</i>     | yes (no)             | 2-7(-8)            | yes (no)             | glandular               | 3.5-7(-8)            | (15-)16-18(-20)        | 1-1.3                 |
| <i>P. saxosorum</i>     | no                   | 3-19               | no                   | glabrous                | 3.5-8                | 17-25(-30)             | 1-1.5                 |
| <i>P. scariosus</i>     | no                   | 2-15(-23)          | no                   | glandular<br>(glabrous) | (3-)4-9(-13)         | (15-)16-30(-33)        | (1.3-)1.5-2.2(-2.6)   |



glabrous or glabrate except sometimes for the margins and midvein, the basal leaves tend to be narrow and deciduous, and the corolla lobes are often long and wide.

Variety *fremontii* is typically found associated with *Artemisia tridentata* on relatively well developed soils. Variety *glabrescens* is found on partly barren, south facing slopes of Green River shale with *Amelanchier*, *Chrysothamnus*, and *Holodiscus* on poorly developed soils. The main elevational range of the two varieties is nearly the same, about 1770 to 2500 m, but var. *fremontii* has been found down to 1525 m. The habitats are strikingly different, however, and var. *glabrescens* is found only at the southernmost edge of the range of var. *fremontii* (Fig. 2).

Variety *glabrescens* also resembles *P. gibbensii* Dorn but lacks the glands in the inflorescence and tends to have broader leaves. *Penstemon scariosus* Pennell is also similar but has glabrous stems below the inflorescence and the hairs on the anthers are generally longer and more copious and the anther sacs are longer. *Penstemon saxosorum* Pennell likewise has glabrous stems below the inflorescence. A comparison of selected features for these taxa is presented in Table 1.

#### ACKNOWLEDGMENTS

We thank Ronald Hartman, curator of RM, for use of those facilities, the curators of COLO and CS for allowing study of their specimens, and the reviewers of the original manuscript, Noel Holmgren and William Weber, for their helpful comments. Field work was supported by Bureau of Land Management Contract #CO-910-CT7-016.

(Received 12 Apr 1989; revision accepted 9 Apr 1990.)



# MARITIME STRESS TOLERANCE STUDIES OF CALIFORNIA DUNE PERENNIALS

BRIAN H. FINK and JOY B. ZEDLER

Biology Department, San Diego State University,  
San Diego, CA 92182

## ABSTRACT

Experimental evidence indicates that *Camissonia cheiranthifolia* ssp. *suffruticosa*, a coastal dune perennial, is excluded from the strandline community due to intolerance of seawater inundation and sand burial. The strandline dune species *Abronia maritima* and *Ambrosia chamissonis* were tolerant of all maritime stresses tested.

## RESUMEN

Evidencia experimental indica que *Camissonia cheiranthifolia* ssp. *suffruticosa*, una especie terrenal de médano costero, está excluido de la comunidad de encalle dado su intolerancia de inundación de agua salada y entierro arenal. Las especies de encalle en médanos costeros *Abronia maritima* y *Ambrosia chamissonis* toleraron todas las pruebas de tensión marítima echas [en ellas].

The goal of this study was to identify environmental stresses that are responsible for the observed zonation patterns of three dune species (*Abronia maritima*, *Ambrosia chamissonis*, and *Camissonia cheiranthifolia* ssp. *suffruticosa*) in coastal San Diego County. In the current (although disturbed) zonation pattern, *Abronia maritima*, *Ambrosia chamissonis*, and *Carpobrotus* spp. dominate the foredune environment (under occasional tidal influence); *Camissonia cheiranthifolia* ssp. *suffruticosa*, *Abronia umbellata*, and *Lotus nuttalianus* grow in the backdunes (not typically washed over); and a coastal scrub community composed of *Lotus scoparius*, *Eriogonum fasciculatum*, and *Encelia californica* occurs further inland.

Environmental stress (defined as any condition reducing plant growth) is not uniform among coastal dune habitats. Many factors vary with proximity to the ocean, so that plants at the driftline routinely encounter greater stress than those inland (Avis and Lubke 1985; Barbour 1978; Lee and Ignaciuk 1985; Oosting and Billings 1942). Species are distributed in rough bands parallel to the coast (Doing 1985; Donnelly and Pammenter 1983; Nakanishi and Fukumoto 1987; and Orme 1973); the zonation is most easily explained by different tolerance limits to these maritime stresses. This species zonation is not stable, however. Distribution limits may expand during benign conditions, but be curtailed by a storm or other disruption. Thus, the distributional patterns of coastal plants may relate



more to the length of time since the last disturbance than to average conditions at a particular location.

Environmental factors not only vary inland from the beach, but along the coastline as well. Quantities and types of maritime stresses received are unique for each beach depending on such factors as microtopography (Barbour 1978), directional exposure (Travis 1977), recreational use (if any), sand supply, etc. In San Diego County, for example, south-facing beaches may be sheltered from winter storms that approach from the northwest, resulting in less storm-generated disturbance. In addition, coastal canyons funnel episodic Santa Ana winds, causing certain beaches to experience more sand movement than others. Generally, due to low average wind velocities at this latitude (Calif. Dept. Water Resources 1985), wind-mediated stresses (seaspray deposition, sand movement, and sandblasting) are probably not as important as storm-generated ones (erosion, seawater inundation, and sand dumping).

The literature suggests that salt toxicity is limiting to coastal plants (Donnelly and Pammenter 1983; Oosting and Billings 1942; Barbour and DeJong 1977; Boyce 1954; and Malloch 1972). This may result from two processes: seawater enters plants that have been severed by crashing waves and moving sand; seaspray enters the plant after epidermal cells have been sandblasted.

This study evaluated the effects of three stresses (seawater inundation, sand burial, and seaspray) that may limit coastal dune plant growth and survivorship at this latitude. Sea spray deposition was monitored in the field and an overwash experiment took place on a restored dune. Sand burial and nutrient effects were evaluated experimentally at the Pacific Estuarine Research Laboratory (PERL).

Three species of native dune perennials were examined experimentally. *Abronia maritima* (red sand verbena) is a succulent prostrate forb with a long taproot. *Ambrosia chamissonis* (beach bur), another long-lived deep-rooted perennial that is more common than *Abronia* on local beaches, has been characterized as an aggressive foredune builder (Purer 1936; Cooper 1967). *Camissonia cheiranthifolia* ssp. *suffruticosa* (beach evening primrose), a shorter-lived, upright woody perennial, occurs as a pioneer species predominantly on backdunes (Purer 1936). All 3 species have long taproots that quickly penetrate the surface substrate to reach permanently moist sand (up to 2–3 m as investigated at the Silver Strand State Park beach).

## METHODS

This study was done in southern San Diego County, California (32°30'N, 117°09'W): field work at the Tijuana Estuary/Border Field State Park and the Silver Strand State Park, and experimental work



at PERL. Border Field State Park is located on the coast, immediately north of the U.S.–Mexican border. PERL is located east of Border Field State Park, 1 km inland of the Tijuana Estuary river mouth and within the Tijuana River National Estuarine Research Reserve. The Tijuana Estuary barrier beach is highly dynamic due to the presence of the estuary mouth and an artificially narrow beach. Dune wash-over events frequently move sediments into estuary channels, cutting off tidal flow. Management agencies have repeatedly dredged sediments from these channels to maintain the tidal prism necessary to keep the estuary mouth open; these spoils were placed on the upper beach. Vegetation is sparse due to human trampling and wash-over events. The Silver Strand State Park beach is more stabilized and characterized by larger dunes vegetated with *Carpobrotus* spp.

Seaspray deposition was monitored at Border Field State Park. Experimental plantings on the Tijuana Estuary barrier dune were washed over many times during the winter months, providing useful data on the effects of seawater inundation. The nutrient and burial experiments, carried out at PERL, sought specific responses to individual stresses (sand burial and varying levels of nutrients including seawater).

*Monitoring of seaspray.* Seaspray was collected on 9 filter paper traps (Whatman paper, round with 12.5 cm diameter) as used by Barbour and DeJong (1977), placed vertically 0.3 m above the sand substrate in areas void of vegetation. Traps were left in the field for up to one week at a time, except when a severe wind event occurred when traps were left out for 24 hours. Filters were collected and soaked in 20 ml of distilled water for 5 minutes, and conductivity of the water was measured with a Labline mho meter.

*“Natural” wash-over experiment.* An experiment was conducted on the restored dune north of the Tijuana River mouth. This dune was inadvertently constructed too close to the surf but proved ideal for quantifying the effects on dune vegetation caused by wash-over events (seawater inundation and storm induced sand erosion/accretion). Due to the intensity of the storm surge and the large amount of sand displaced, the amount of water and sand that the system received was not quantified. However, dune elevations were taken monthly (Fink 1987).

To protect experimental plants from heavy recreational use, three replicate 10 × 10-m areas were enclosed with hogwire fencing. The 10-cm openings between wires did not impede sand flow. Thirty-six (1-month-old) seedlings were planted on 14 June 1986 within each enclosure: 12 each of *Ambrosia chamissonis*, *Abronia maritima*, and *Camissonia cheiranthifolia*. Plantings were approximately 40 m inland from 0.0 mean lower low water (MLLW). All seedlings were



drip irrigated for 2 weeks to facilitate establishment. Following this period, plants received approximately 8 liters of water/week only when dry conditions prevailed. During the first month, plants lost to mortality were replanted. Monitoring of the planted vegetation began 7 July 1986 and ended 15 March 1987. Survivorship and canopy volume were quantified monthly or after a wash-over event. The site was visited at least twice per week.

*Sand burial experiment.* Dune vegetation may be buried by either wash-over or wind-mediated deposits of sand. A single wash-over event can dump large amounts of sand (up to 2 m) on the vegetation and bury entire plants. The maximum amount of sand deposition is dictated by storm intensity. In contrast, wind blown sand grains are physically impeded during "sand accretion." Here, sand accumulation is related to the height of plants. When all vegetative portions are covered, sand grains are no longer physically impeded. For this reason, wind-mediated sand accretion may result in much less sand deposition at low-wind latitudes such as San Diego County, compared to the "sand dumping" process. In addition, sand accretion does not involve physical contact with the surf.

The sand dumping and sand accretion processes differ in the rate of sand deposition and have different effects on the vegetation. An experiment was designed to compare tolerances of the three species under study to high (as in sand dumping) and low (more similar to sand accretion) deposition rates. The experiment was conducted outdoors at PERL. A 2.5-m deep trench was excavated down to a substrate of coarse grain river sand, then filled with 2 meters of native dune sand taken from the Silver Strand State Park beach. Nine equal  $1 \times 1$ -m plots were then created within this trench with plastic sheet dividers secured with wooden stakes. These plastic "walls" prevented contamination of adjacent plots from sand addition treatments. Although no experimental plants were shaded, the plastic may have resulted in higher air and soil temperatures due to heat absorption and reduced wind flow; this was not quantified.

Each plot was planted on 10 April 1986 with three plants of all three species (nine plants), which were randomly assigned. Plants were six months old at planting time and were not fertilized for the duration of the experiment. The soil substrate contained very little organic matter, with the exception of some partially decomposed *Carpobrotus* spp. stems. Plants were watered (soaked) with tap water weekly for the first 6 weeks, then monthly.

Treatment levels of 0 cm, 5 cm and 10 cm of sand addition per month were assigned randomly to the nine plots. These treatments were based on observations of accretion/erosion rates following wind events at local beaches over the previous three years. Three burial treatments were administered starting on 19 May 1986 and ending



4 August 1986. Sand for this purpose was obtained the day of treatment application from the restored dunes at the Tijuana Estuary. Survivorship was quantified on 10 March 1987 by excavating all plants.

*Seawater and nutrient experiment.* The purpose of this experiment was to test for a response (positive or negative) to seawater and inorganic fertilizer. It is quite possible that small quantities of seawater are beneficial to coastal plants whereas larger quantities limit growth, thus contributing to the zonation pattern. The effects of seawater were tested both as spray on leaves (simulating seaspray) and as liquid on roots (simulating wash-over).

Plants for this experiment were germinated in beds. When they reached the "third-leaf stage" they were transplanted (on 10 June 1986) to standard 1-gallon (3.8 liter) pots (one plant per pot) with native dune sand from the Silver Strand State Park and grown outdoors at PERL. All experimental plants were protected from receiving additional seaspray from the ocean by placing them on the lee side of a trailer.

The following four treatments were administered to three species with four-fold replication of pots on 10 July 1986, and every two weeks thereafter for 16 weeks:

- 1) Fertilized with 80 g Osmocote brand slow-release fertilizer per pot;
- 2) Watered with 30 ml of locally collected seawater to simulate seawater inundation;
- 3) Leaves sprayed with 2 ml locally collected seawater applied to the foliage via an atomizer to simulate seaspray deposition;
- 4) Control; no nutrients.

Treatment #1 was administered only once at the beginning of the experiment to the surface soil; treatments #2 and #3 were repeated every 2 weeks. In the seawater treatment, seawater was added directly to each pot. Prior to the spray treatment application, the soil surface was covered with a paper towel to prevent any spray from entering the soil. Two ml of seawater was chosen for spraying to mimic natural amounts accumulated on the beach. To determine if this quantity was realistic, plants with filter paper traps situated within the canopy were sprayed with varying amounts of seawater. Traps receiving the 2 ml treatment captured 1600 micromhos/cm of salt. Since this treatment was to be administered every 2 weeks, the daily average was 114 micromhos/cm/day. This quantity was found to be at the lower end of the range of salts collected on filter paper traps observed in the field.

After each treatment application, all control, fertilized, and sea-sprayed plants were watered with 30 ml of tapwater to compensate



TABLE 1. SEASPRAY QUANTIFICATION. Relative amounts of seaspray deposited per 24 hour period on filter paper traps in 3 dune microhabitats (windward, ridge, and lee) on 5 sampling dates; values are in micromhos/cm.

|          |      | Sampling date |              |             |              |             | Mean |
|----------|------|---------------|--------------|-------------|--------------|-------------|------|
|          |      | 19 Mar<br>86  | 14 Apr<br>86 | 9 May<br>86 | 17 Jan<br>87 | 2 Mar<br>87 |      |
| Windward | mean | 1068          | 1183         | 1231        | 1448         | 2240        | 1459 |
|          | n    | 2             | 3            | 2           | 3            | 3           |      |
|          | SE   | 41            | 231          | 396         | 54           | 762         | 187  |
| Ridge    | mean | 331           | 518          | 808         | 2250         | 1833        | 1297 |
|          | n    | 2             | 2            | 2           | 3            | 3           |      |
|          | SE   | 51            | 100          | 39          | 76           | 36          | 337  |
| Leeward  | mean | 170           | 187          | 110         | 413          | 1143        | 467  |
|          | n    | 2             | 2            | 2           | 3            | 3           |      |
|          | SE   | 99            | 55           | 10          | 38           | 422         | 153  |

for the water added to the seawater addition treatment. Plants were rotated prior to treatment application. After 8 treatment applications (16 weeks), the pots were emptied, the stems cut from the roots, and both plant portions washed and bagged separately. These samples were oven-dried at 50°C for 36 hours and weighed.

Seawatered plants were flushed with 50 ml of tap water every 4 weeks to prevent a salt crust from forming on the soil surface (high soil salinities are not normally encountered in the dune substrate). Observations of dune soils at the Silver Strand State Beach before and after precipitation events indicate that 1.5–2.0 inches of rain are required to reach depths greater than 0.5 m. Under average precipitation conditions in San Diego County, 3–4 winter storms produce precipitation with potential for flushing the soil horizon. This would average out to 1 storm/month during the rainy season; thus monthly flushing was chosen for the experimental pots.

## RESULTS

*Tolerance to seawater as seaspray.* Monitoring of seaspray deposition revealed that the protected lee slopes of coastal dunes experience lesser quantities of this stress than the windward or ridge slopes (Table 1). This is consistent with the findings of Barbour (1978) who quantified seaspray deposition in northern California. However, due to much higher daily wind velocities in northern California (Fig. 1), one would anticipate lower seaspray deposition rates in southern California.

The seaspray treatments used in the nutrient experiment were sufficient to scorch *Camissonia* and *Ambrosia*; there was no difference in biomass between seasprayed plants and the controls. Al-



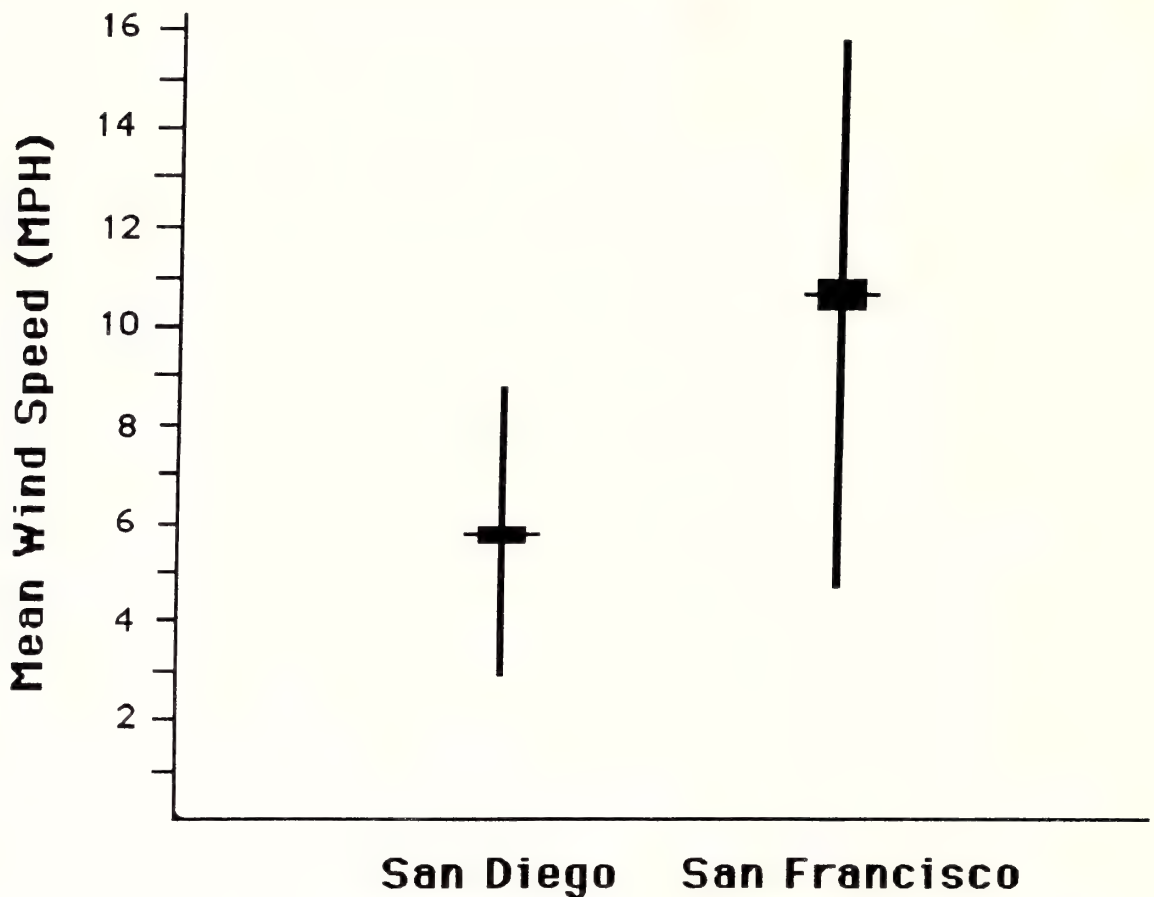


FIG. 1. Contrasting wind speeds (1960–1978) for San Diego (32°42'N) and San Francisco (37°37'N) computed from mean monthly wind values.  $n = 12 \text{ months} \times 19 \text{ years} = 228$ . Horizontal lines are means, rectangles represent  $\pm 1$  SE; vertical lines are extreme mean monthly values recorded over the 19-year study period. Data from Calif. Dept. Water Resources (1985).

though *Camissonia* leaves were scorched, plants produced significantly more flowers under this treatment (Kruskal-Wallis test,  $p < 0.05$ ; Fig. 2); there was no significant effect on flowering or survival of *Ambrosia* or *Abronia*.

*Tolerance to seawater in a wash-over event.* Most of the restored dune was washed over many times during the course of this “natural” field experiment. The first wash-over event occurred during the storm of 4 December 1986 (Fig. 3). Although it is uncertain how many times the barrier dune was washed over during this storm season, all 3 plots were inundated at least once, and plots 1 and 2 at least three times. Plants in plot 2 experienced the harshest contact with the surf; here twenty cm of sand was eroded and entire plants were swept away.

Seedlings were probably well established before the storm, based on observations at the adjacent Silver Strand State Park, where excavated seedlings had reached permanently moist sand (1–2.8 m from the surface) within 6 months. Seven (of twelve total) *Ambrosia* plants in plot 2 were washed away, whereas all twelve *Ambrosia*



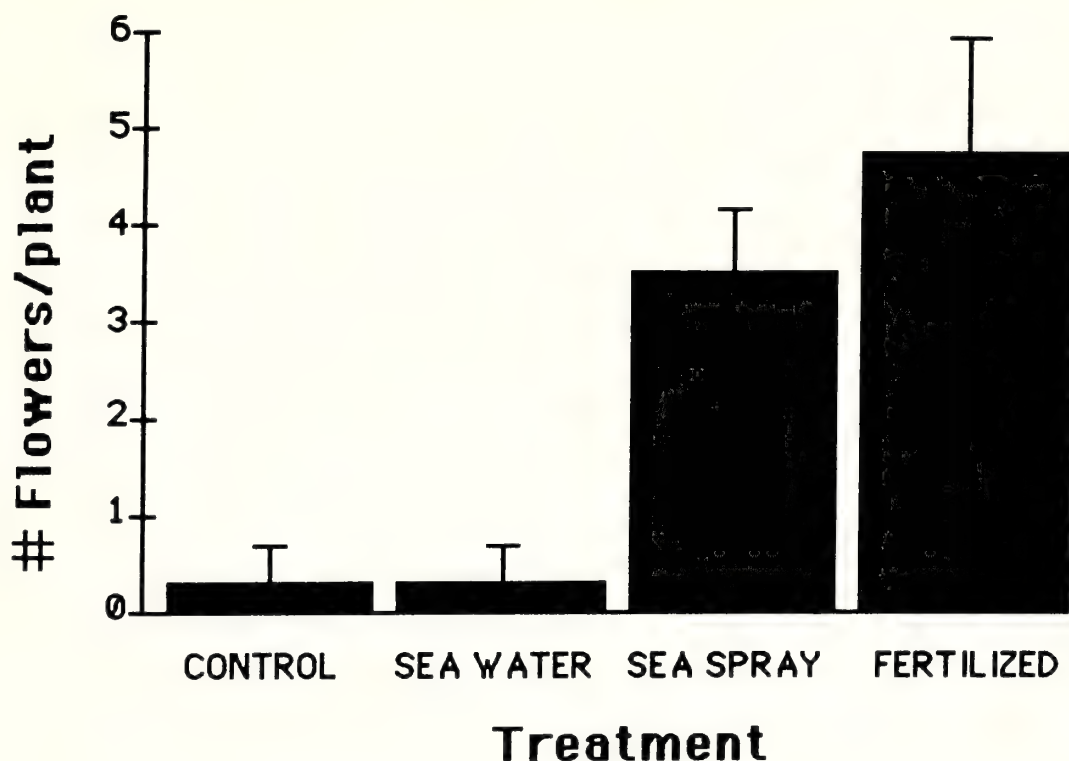


FIG. 2. Numbers of flowers/plant produced by *Camissonia cheiranthifolia* ssp. *suffruticosa*, for each treatment administered in the fertilizer experiment. Error bars are  $\pm 1$  SE;  $n = 4$ .

plants persisted in both plots 1 and 3. Due to these between-plot differences in storm effects, there was high variability in the survivorship curves for February and March (Fig. 3). *Abronia* survivorship decreased steadily from the planting date but did not coincide with storm wash-overs. Mortality likely resulted from overwatering; *Abronia* grew best when planted  $> 1$  m from a drip emitter.

There was a second wash-over event on 17 January 1988 (cf. *Shore & Beach* 57[4], special storm issue) that severely eroded the barrier dune at the Tijuana Estuary. Observations following this extreme storm (Fink 1989) showed that *Abronia* has the ability to withstand seawater inundation: *Ambrosia* and *Abronia* resprouted 1 week following this event and resumed growth thereafter. All *Camissonia* were killed; mature plants remained brown and did not resprout. All *Camissonia* seedlings were also destroyed and no new ones appeared in spring 1988.

Results from both "natural" experiments indicate that *Camissonia* cannot withstand repeated seawater inundation. This may explain why it is unable to grow in the strandline environment, where wash-over events are common. However, *Camissonia* growing in the third plot, which was washed over only once, did not perish, indicating that this species can tolerate other maritime stresses such as sand erosion and seaspray deposition (as well as limited quantities of seawater inundation).

Further evidence of *Camissonia*'s inability to tolerate wash-over



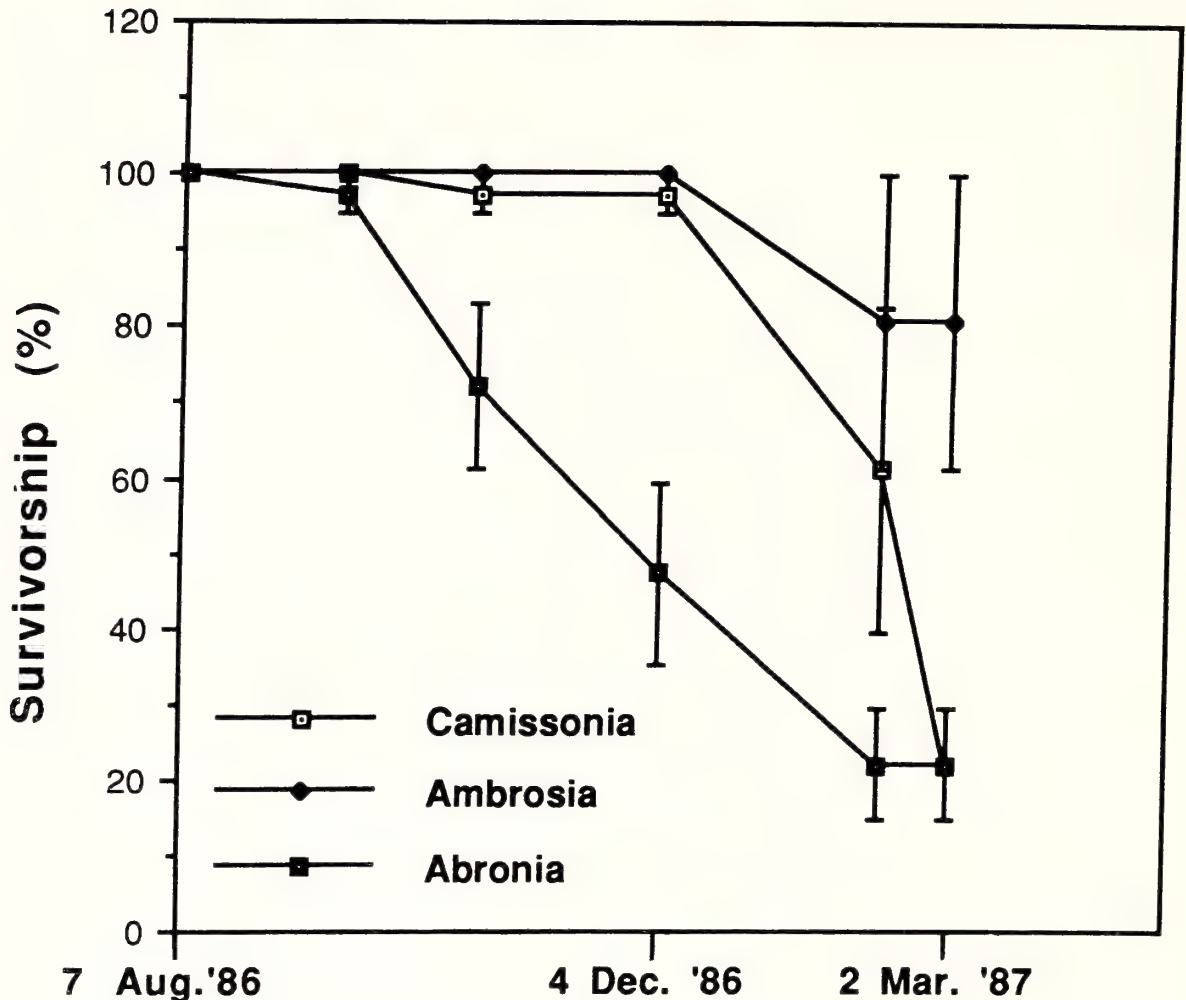


FIG. 3. Survivorship of three species of dune perennials over a 245-day period on the restored dune at the Tijuana Estuary. Note that *Camissonia* and *Ambrosia* mortality coincided with the advent of winter wash-over events (4 Dec 86).  $n = 34$  *Camissonia*, 18 *Abronia*, and 36 *Ambrosia* for all 3 plots combined.

events comes from the nutrient experiment (Fig. 4). Roots of *Camissonia* subjected to seawater inundation were significantly smaller than those of the control plants (one-way ANOVA,  $p < 0.05$ ). Treatments were not significantly different from controls for *Abronia* and *Ambrosia*, with the exception of the fertilizer treatment which increased biomass for both species.

Evaluation of the water table below *Camissonia* growing in a dune slack at the Silver Strand State Park beach indicates that *Camissonia* roots may tolerate exposure to brackish water (less than 5 ppt; Fig. 5). Here the depth to water table fluctuated from 0.97 m in winter to 1.38 m during the summer months (Fink 1987). Roots were excavated at 1.2 m in summer, 1986, indicating that this species may tolerate some exposure to brackish water during the winter months.

*Tolerance to sand burial.* The three species of dune plants used for this experiment all had different responses to the sand burial treatments (Fig. 6). *Ambrosia* was the most tolerant, and *Camissonia*



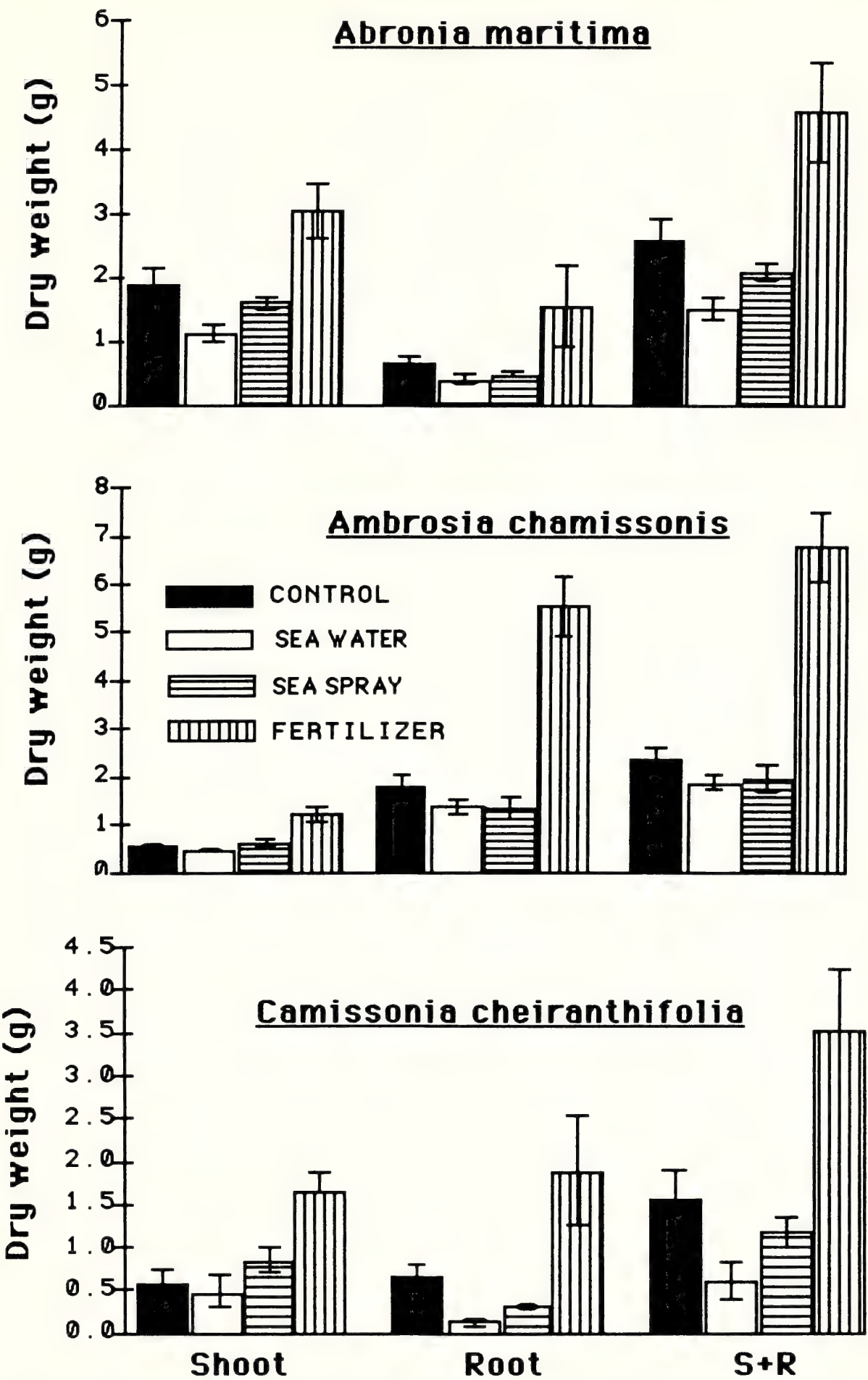


FIG. 4. Response of three species of dune plants to 4 nutrient treatments. Roots of *Camissonia* plants receiving the seawater treatment weighed significantly less than controls. Error bars are  $\pm 1$  SE; n = 4.



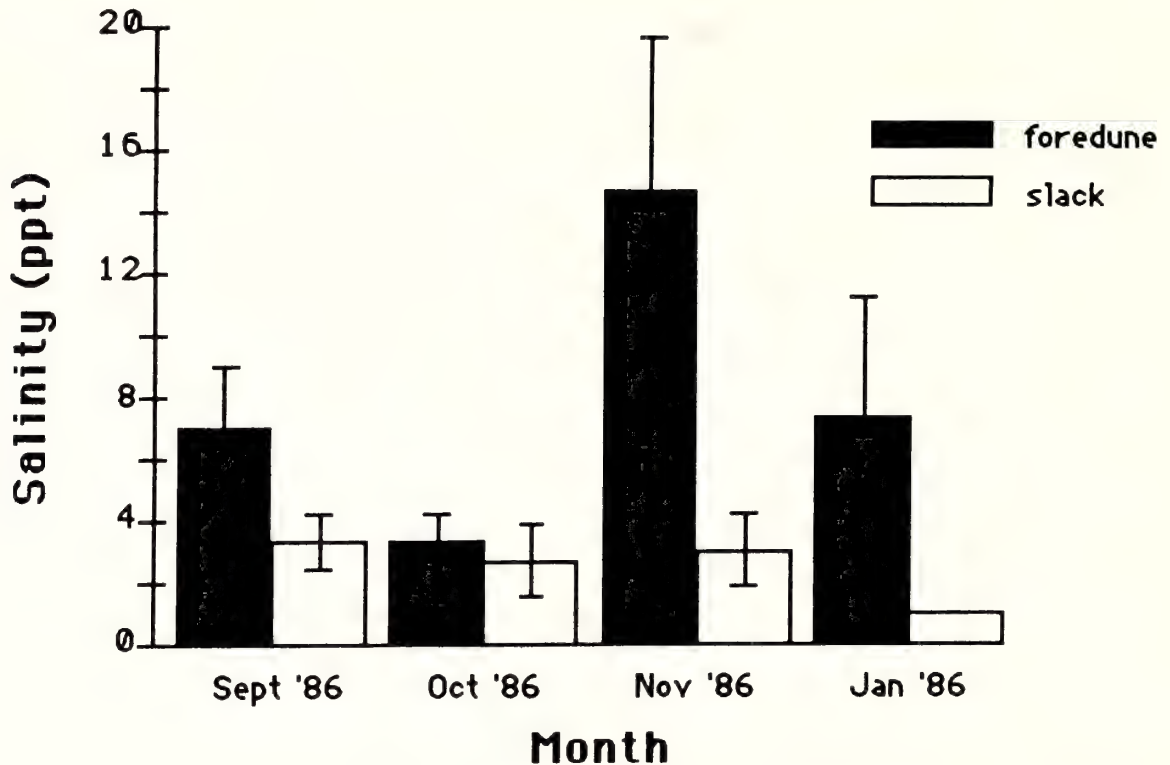


FIG. 5. Salinities in parts per thousand in water table samples taken from foredune and slack sampling sites at the Silver Strand State Park beach. Salinities were taken with a refractometer; samples were taken at 3 m depth for the foredune and 1 m in the slack zones. Error bars are  $\pm 1$  SE;  $n = 3$ .

the least. Inspection of the growth responses throughout the experiment revealed that *Ambrosia* could sprout up through a complete covering of sand; it survived the heaviest burial treatment (10 cm/month; 30 cm total). *Abronia* growth continued only while the apical meristem was not completely covered. Specimens of *Camissonia* died when the central rosette was covered (and remained so) by approximately 20 cm of sand, although the flowering shoots remained above ground. This indicates that *Abronia* and *Camissonia* are tolerant of sand accretion (wind-mediated), but cannot survive "sand dump" (storm-induced). These findings are also supported by Cunniff (1984), who studied the foredune vegetation at Point Mugu (Ventura County, California) before and after the intense storm of February 1983. At Point Mugu, *Ambrosia* emerged through a 1 m layer of wash-over sand, whereas *Camissonia* perished.

#### DISCUSSION

This study indicates that, in southern California, a distinct zone of beach vegetation is maintained by storm wash-over events. Wind-mediated stresses probably did not limit growth or survivorship of the three species studied in 1986 (or 3 years thereafter). Within the zone of inundation, typically only 4 or 5 strandline species are present following wash-over. These plants could be thought of as "sea-



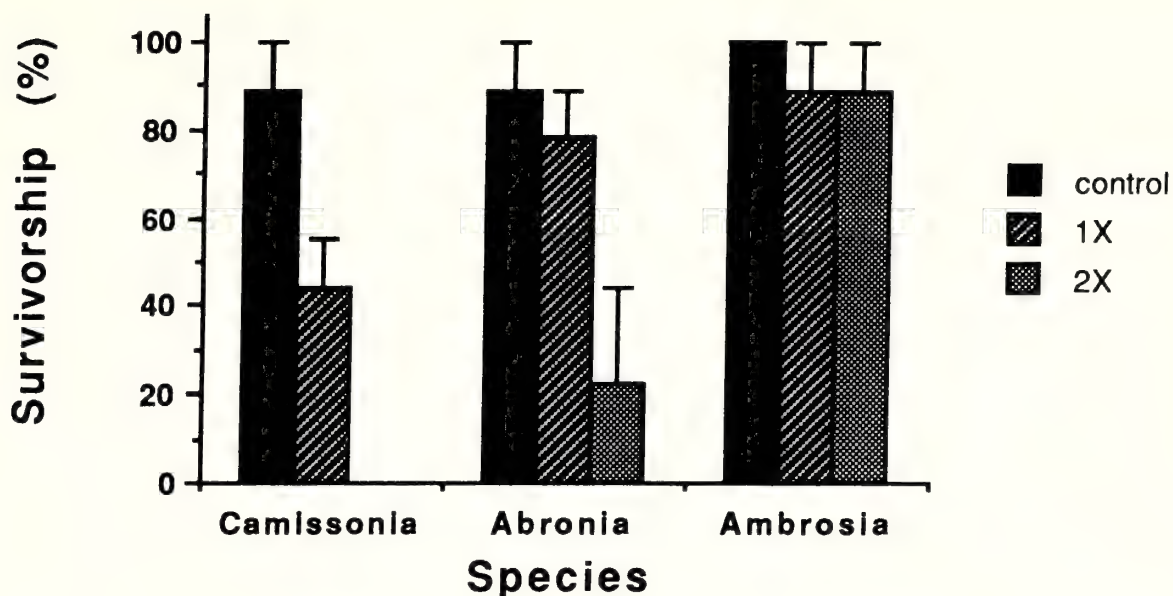


FIG. 6. Percent survivorship for 3 species of dune perennials (six months of age) grown under 3 sand addition treatments: control = no sand addition, 1× = 5 cm/month, for a total of 15 cm after three treatments; 2× = 10 cm/month, for a total of 30 cm after three treatments. Error bars are  $\pm 1$  SE;  $n = 9$  plants. Percent survivorship for *Camissonia* subjected to the 2× treatment was zero (no bar shown on this graph).

sonal halophytes” due to their ability to deal with inundation for a portion of the year. Others dune species, such as *Camissonia cheiranthifolia* ssp. *suffruticosa* are removed during this dynamic process.

Further inland, out of reach of the storm waves, dune plant species may be salt stressed, but from seaspray. Although the quantity of salts may be substantially less than at the strandline, the chemical composition is potentially more damaging due to ion separation when blown inland (Clayton 1972). In addition, seaspray deposition is chronic in nature, occurring over the entire season. Plants tolerant of chronic seaspray have been termed “aerohalophytes” (Rozema et al. 1982). Microsites within the inland zone may provide some protection from seaspray, allowing intolerant species to occur.

Further experimentation would be appropriate to determine if a “zone of aerohalophytes” is maintained by the effects of seaspray, eliminating plant species more typically found inland (dune scrub, coastal sage scrub, and weedy glycophyte species). Preliminary evidence suggests that this is the case, as mortality of species such as *Lotus scoparius*, *Eriogonum fasciculatum*, and *Melilotus indicus* has been observed after intense wind events (20 knot winds for at least 4 hours). This zone may be less distinct in San Diego County compared with latitudes where daily wind events cause significantly more salt stress.

Examination of wind patterns (Calif. Dept. Water Resources 1985; Goodridge et al. 1979) suggests that coastal southern California is relatively calm and that strong winds occur only rarely during winter



storms and Santa Ana (dry, offshore) wind events. Even during these times, seaspray deposition is minimal. Winter storms are usually accompanied by precipitation, which reduces salt accumulation, whereas Santa Ana winds prevail from the E-NE and are not likely to contain seasalt. Cooper (1967) stated that south of Point Conception (200 km north of San Diego County) the wind "both in velocity and prevailing direction, is relatively inefficient in moving sand from the beach inland." The coast of northern California experiences much higher daily wind velocities; wind mediated stresses would more likely limit dune plants at this latitude.

Seaspray deposition was not sufficient to cause plant mortality during this study. With the low wind velocities that are characteristic of this latitude, seasalts may actually enhance growth (or at least fecundity) of certain dune species. Increased flowering was observed for *Camissonia* when it was experimentally sprayed with seawater.

Other researchers have documented salt-stimulated growth of coastal plants (Lee and Ignaciuk 1985; Okusanya 1979; Rozema et al. 1983), although from seawater inundation rather than seaspray. The water table sampled at the Silver Strand State Park was brackish; perhaps mature plants obtain nutrients from seawater moving laterally below ground.

This study suggests that storm-generated stresses are more limiting than wind-generated ones for the three species of plants tested, using well-established seedlings. However, the reverse might be true for newly germinated seedlings. Seedling establishment is perhaps the most vulnerable stage of the life cycle of the dune perennials under study. DeJong (1979) has stated that *Abronia* and *Ambrosia* can become established in southern California only in years with late spring and early summer precipitation events. Once germination occurs following winter rains, seedling roots must grow at a pace that keeps up with a layer of moist sand that recedes as the surface layers dry out. Dune soils sampled at the Silver Strand State Park dropped to near 1% water (by weight) during the summer months in the upper 0.5 m (Fink 1987).

Sand movement can also be problematic for seedlings; they may be eroded away in exposed areas or buried in the dune swales or the lee of hummocks. Dead seedlings of *Cakile maritima* (third leaf stage) were observed after 10 cm of sand was eroded by a Santa Ana wind event. Thus at this latitude, wind generated stresses may be more limiting to growth and survival of seedlings than to mature plants. Additional studies of newly germinated seedlings are needed to improve our understanding of distribution patterns.

#### ACKNOWLEDGMENTS

This research was sponsored by NOAA, Office of Coastal Zone Research and Management, Estuarine Sanctuary Programs Division, Washington, DC (Grant #NA86AA-D-CZO16). The authors wish to thank David Keil, Frank Davis, and an



anonymous reviewer for their helpful suggestions and comments and Ricardo Martinez-Lara for translating the abstract into Spanish.

#### LITERATURE CITED

- AVIS, A. M. and R. A. LUBKE. 1985. The effect of wind-borne sand and salt spray on the growth of *Scirpus nodosus* in a mobile dune system. *S. African J. Bot.* 51: 100–110.
- BARBOUR, M. G. 1978. Saltspray as a micro-environmental factor in the distribution of beach plants at Point Reyes, California. *Oecologia* 32:213–224.
- and T. M. DEJONG. 1977. Response of West Coast beach taxa to salt spray, seawater inundation and soil salinity. *Bull. Torrey Bot. Club* 104:29–34.
- BOYCE, S. 1954. The saltspray community. *Ecol. Monogr.* 24:29–67.
- CALIFORNIA DEPARTMENT OF WATER RESOURCES. 1985. California wind atlas. Final report to the California Energy Committee, Contract #P-500-82-044, Sacramento, CA.
- CLAYTON, J. L. 1972. Salt spray and mineral cycling in two California coastal ecosystems. *Ecology* 53:74–81.
- COOPER, W. S. 1967. Coastal dunes of California. *Geol. Soc. Amer. Mem.* 104. Boulder, CO.
- CUNNIFF, S. E. 1984. Vegetation patterning on a southern California barrier beach. M.S. thesis. Univ. California, Los Angeles.
- DOING, H. 1985. Coastal fore-dune zonation and succession in various parts of the world. *Vegetatio* 61:65–75.
- DEJONG, T. M. 1979. Water and salinity relations of California beach species. *J. Ecol.* 67:647–663.
- DONNELLY, F. A. and N. W. PAMMENTER. 1983. Vegetation zonation on a natal coastal sand-dune system in relation to salt spray and soil salinity. *S. African J. Bot.* 2:46–51.
- FINK, B. H. 1987. Stress tolerance of three coastal dune perennials. M.S. thesis. San Diego State Univ., San Diego, CA. 67 pp.
- . 1989. Effects of dune overwash during the January 18, 1988 storm at the Tijuana Estuary, San Diego, California. *Shore & Beach* 57:41–43.
- GOODRIDGE, J. D., H. RHODES, and E. G. BINGHAM. 1979. Windstorms in California. Dept. of Water Resources, Division of Planning, Sacramento, CA. 34 pp.
- LEE, J. A. and R. I. IGNACIUK. 1985. The physiological ecology of strandline plants. *Vegetatio* 62:319–326.
- MALLOCH, A. J. C. 1972. Salt-spray deposition on the maritime cliffs of the Lizard Peninsula. *J. Ecol.* 60:103–112.
- NAKANISHI, H. and H. FUKUMOTO. 1987. Zonation of coastal vegetation and coastal topography in southern Japan. *Jap. J. Ecol.* 37:197–207.
- OKUSANYA, O. T. 1979. An experimental investigation into the ecology of some maritime cliff species. *J. Ecol.* 67:579–590.
- OOSTING, H. J. and W. D. BILLINGS. 1942. Factors affecting vegetational zonation on coastal dunes. *Ecol.* 23:131–142.
- ORME, A. T. 1973. Coastal dune systems of northwest Baja California, Mexico. Technical Report 0-73-1. Office of Naval Research, Arlington, VA.
- PURER, E. A. 1936. Studies of certain coastal sand dune plants of southern California. *Ecol. Monogr.* 6:1–87.
- ROZEMA, J., F. BIJL, T. DUECK, and H. WESSELMAN. 1982. Salt-spray stimulated growth in strand-line species. *Physiol. Pl. Copenhagen* 56:204–210.
- , T. DUECK, H. WESSELMAN, and F. BIJL. 1983. Nitrogen dependent growth stimulation by salt in strand-line species. *Acta Ecol. Pl.* 4:41–52.
- TRAVIS, R. 1977. The effects of aspect and exposure on the growth of dune grasses in Cape Hatteras National Seashore. *Int. J. Biometeorol.* 21:217–226.

(Received 9 Aug 1989; revision accepted 9 Jan 1990.)



## NOTES

ADDITIONS TO THE VASCULAR FLORA OF YELLOWSTONE NATIONAL PARK, WYOMING. — Continued floristic work based at the Rocky Mountain Herbarium (RM) has resulted in 23 new records for the vascular flora of Yellowstone National Park. Field work in the northern Absaroka Range was done by Hartman and Nelson in 1985; the southwest Absarokas were collected separately and together by Hartman and Snow in 1987 and 1988 (Snow 1989, Floristics of the headwaters region of the Yellowstone River [Wyoming], M.S. thesis, Univ. Wyoming). Both areas had been virtually unbotanized as they are remote, are inaccessible except on foot, and are composed mostly of rugged volcanics reaching over 3200 m in elevation. These records are from a total of 850 collection numbers. Four additional specimens encountered in RM are also cited.

All 23 reports represent range extensions of these taxa in Wyoming (R. D. Dorn 1988, Vascular plants of Wyoming). Yellowstone distribution records are based on D. G. Despain (1975, Field key to the flora of Yellowstone National Park) and G. P. Hallsten, Q. D. Skinner, and A. A. Beetle (1987, Grasses of Wyoming, 3rd ed.). Nomenclature follows Dorn (1988) and the Wyoming Species List (B. E. Nelson and R. L. Hartman unpubl., at RM); voucher specimens are deposited at RM.

*Senecio fuscatus* Hayek (Asteraceae). — Park Co., above Hoodoo Basin at the head of Lamar River between Lamar Mountain and Hoodoo Peak, alpine meadows and slopes, T55N R108W sect. 35, 3108–3168 m, 22 Jul 1985, *Nelson and Hartman 12761*.

*Senecio werneriiifolius* (A. Gray) A. Gray var. *alpinus* (A. Gray) Dorn (Asteraceae). — Park Co., on the divide 10–15 air km SSE of Silver Gate, MT, alpine meadows and rocky slopes, T57N R108W sect. 9, 16, 21, 2987–3230 m, 27 Jul 1985, *Hartman 21571*; Republic Pass, ca. 5 km SE of Amphitheater Mountain, dry meadows and slopes above treeline, T57N R108W sect. 5, 3048 m, 14 Jul 1985, *Nelson and Hartman 12455*; near summit of The Thunderer, rocky slope, T57N R109W sect. 20, 3139 m, 13 Jul 1899, *A. Nelson and E. Nelson 5822* (all collections verified by R. D. Dorn, 1988).

*Taraxacum eriophorum* Rydb. (Asteraceae). — Park Co., on the divide 10–15 air km SSE of Silver Gate, MT, alpine meadows and rocky slopes, T57N R108W sect. 9, 16, 21, 2987–3230 m, 27 Jul 1985, *Hartman 21594* (collection verified by R. Doll, 1986).

*Eritrichium nanum* (Villars) Schrader ex Gaudin var. *elongatum* (Rydb.) Cronq. (Boraginaceae). — Park Co., Hoodoo Basin trail, ca. 10 air km NW of Stinking-water Peak, grassy alpine slopes, T55N R108W sect. 35, 3048–3168 m, 22 Jul 1985, *Hartman 21335*.

*Draba lonchocarpa* Rydb. var. *lonchocarpa* (Brassicaceae). — Park Co., 0.8–1.6 air km S of Republic Pass, alpine meadows and rocky slopes, T57N R108W sect. 5, 2804–2987 m, 26 July 1985, *Hartman 21554*.

*Arenaria nuttallii* Pax ssp. *nuttallii* (Caryophyllaceae). — Park Co., 0.8–1.6 air km S of Republic Pass, alpine meadows and rocky slopes, T57N R108W sect. 5, 2804–2987 m, 26 Jul 1985, *Hartman 21543*; on the divide 10–15 air km SSE of Silver Gate, MT, alpine meadows and rocky slopes, T57N T108W sect. 9, 16, 21, 2987–3230 m, 27 Jul 1985, *Hartman 21564*; Sylvan Pass to Top Notch Peak, spruce-fir and whitebark pine forests and bald summits and rocky outcrops, T52N R110W sect. 19, 20, 29, 30, 2651–3108 m, 29 Jun 1987, *Hartman and Snow 23505*.

*Arenaria rubella* (Wahlenb.) Smith (Caryophyllaceae). — Park Co., The Hoodoos, ca.



3 km SSW of Mammoth, limestone rock crevices, T57N R115W sect. 1, 2286 m, 3 Aug 1985, *R. D. Dorn* 4284; immediately SW of Republic Pass, alpine meadows and grassy slopes, T57N R108W sect. 6, 3139 m, 14 Jul 1985, *Hartman and Nelson* 20812; Hoodoo Basin trail, ca. 10 air km NW of Stinkingwater Peak, grassy alpine slopes, T55N R108W sect. 35, 3048–3168 m, 22 Jul 1985, *Hartman* 21340; on the divide 10–15 air km SSE of Silver Gate, MT, alpine meadows and rocky slopes, T57N R108W sect. 9, 16, 21, 2987–3230 m, 27 Jul 1985, *Hartman* 21577.

*Cerastium beeringianum* Cham. & Schldl. var. *capillare* Fern. & Wieg. (Caryophyllaceae).—Park Co., Hoodoo Basin trail, ca. 10 air km NW of Stinkingwater Peak, grassy alpine slopes, T55N R108W sect. 35, 3048–3168 m, 22 Jul 1985, *Hartman* 21338.

*Silene hitchguirei* Bocq. (Caryophyllaceae).—Park Co., Hoodoo Basin trail, ca. 11 air km NW of Stinkingwater Peak, grassy alpine slopes, T55N R108W sect. 26, 3017–3078 m, 22 Jul 1985, *Hartman* 21355; on the divide 10–15 air km SSE of Silver Gate, MT, alpine meadows and rocky slopes, T57N R108W sect. 9, 16, 21, 2987–3230 m, 27 Jul 1985, *Hartman* 21617.

*Stellaria monantha* Hultén (Caryophyllaceae).—Park Co., immediately SW of Republic Pass, alpine meadows and grassy slopes, T57N R108W sect. 6, 3139 m, 14 Jul 1985, *Hartman and Nelson* 20827; Hoodoo Basin trail, ca. 11 air km NW of Stinkingwater Peak, grassy alpine slopes, T55N R108W sect. 26, 3017–3078 m, 22 Jul 1985, *Hartman* 21370.

*Carex capitata* L. (Cyperaceae).—Park Co., above Hoodoo Basin at the head of Lamar River between Lamar Mountain and Hoodoo Peak, drier hummocks below snowfield, T55N R108W sect. 35, 3108–3168 m, 22 Jul 1985, *Nelson and Hartman* 12725.

*Carex elynoides* Holm (Cyperaceae).—Park Co., Hoodoo Basin trail, ca. 10 air km NW of Stinkingwater Peak, grassy alpine slopes, T55N R108W sect. 35, 3048–3168 m, 22 Jul 1985, *Hartman* 21339; on the divide 10–15 air km SSE of Silver Gate, MT, alpine meadows and rocky slopes, T57N R108W sect. 9, 16, 21, 2987–3230 m, 27 Jul 1985, *Hartman* 21619.

*Carex haydeniana* Olney (Cyperaceae).—Park Co., immediately SW of Republic Pass, alpine meadows and grassy slopes, T57N R108W sect. 6, 3139 m, 14 Jul 1985, *Hartman and Nelson* 20813; Hoodoo Basin trail, ca. 11 air km NW of Stinkingwater Peak, grassy alpine slopes, T55N R108W sect. 26, 3017–3078 m, 22 Jul 1985, *Hartman* 21347, *Hartman* 21373; Teton Co., area between Thorofare Creek and Escarpment Creek, vicinity of Thorofare Ranger Station, dry sandbars of creek, T48N R110W sect. 5 and T49N R110W sect. 28, 33, 34, 2453 m, 4 Jul 1988, *Snow* 3136.

*Carex obtusata* Lilj. (Cyperaceae).—Park Co., immediately SW of Republic Pass, alpine meadows and grassy slopes, T57N R108W sect. 6, 3139 m, 14 Jul 1985, *Hartman and Nelson* 20821; Hoodoo Basin trail, ca. 11 air km NW of Stinkingwater Peak, grassy alpine slopes, T55N R108W sect. 26, 3017–3078 m, 22 Jul 1985, *Hartman* 21387; on the divide 10–15 air km SSE of Silver Gate, MT, alpine meadows and rocky slopes, T57N R108W sect. 9, 16, 21, 2987–3230 m, 27 Jul 1985, *Hartman* 21614.

*Carex pachystachya* Cham. ex Steudel (Cyperaceae).—Yellowstone National Park, wet ground, 26 Aug 1913, *E. Bartholomew* 5216; Park Co., Sedge Creek, T53N R111W sect. 29, 2377 m, 20 Aug 1964, *W. M. Johnson* 499; Republic Pass, ca. 5 km SE of Amphitheater Mountain, dry meadows and slopes above treeline, T57N R108W sect. 5, 6, 3048 m, 14 Jul 1985, *Nelson* 12458 (first two collections verified by R. Whitkus, 1989).

*Gentianella tenella* (Rottb.) Börner (Gentianaceae).—Park Co., on the divide 10–15 air km SSE of Silver Gate, MT, alpine meadows and rocky slopes, T57N R108W sect. 9, 16, 21, 2987–3230 m, 27 Jul 1985, *Hartman* 21600.

*Lloydia serotina* (L.) Reichenb. (Liliaceae).—Park Co., immediately SW of Republic



- Pass, alpine meadows and grassy slopes, T57N R108W sect. 6, 3139 m, 14 Jul 1985, *Hartman and Nelson* 20802.
- Festuca baffinensis* Polunin (Poaceae).—Park Co., Hoodoo Basin trail, ca. 10 air km NW of Stinkingwater Peak, grassy alpine slopes, T55N R108W sect. 35, 3048–3168 m, 22 Jul 1985, *Hartman* 21344.
- Poa secunda* J. S. Presl var. *incurva* (Scribner & T. Williams ex Scribner) Beetle (Poaceae).—Park Co., immediately SW of Republic Pass, alpine meadows and grassy slopes, T57N R108W sect. 6, 3139 m, 14 Jul 1985, *Hartman and Nelson* 20830.
- Potentilla nivea* L. (Rosaceae).—Park Co., Hoodoo Basin trail, ca. 10 air km NW of Stinkingwater Peak, grassy alpine slopes, T55N R108W sect. 35, 3048–3168 m, 22 Jul 1985, *Hartman and Nelson* 21333.
- Saxifraga adscendens* L. var. *oregonensis* (Raf.) Breitung (Saxifragaceae).—Park Co., Hoodoo Basin trail, ca. 11 air km NW of Stinkingwater Peak, grassy alpine slopes, T55N R108W sect. 26, 3017–3078 m, 22 Jul 1985, *Hartman* 21353; on the divide 10–15 air km SSE of Silver Gate, MT, alpine meadows and rock slopes, T57N R108W sect. 9, 16, 21, 2987–3230 m, 27 Jul 1985, *Hartman* 21636.
- Saxifraga flagellaris* Willd. ex Sternb. var. *crandallii* (Gand.) Dorn (Saxifragaceae).—Park Co., Hoodoo Basin trail, ca. 11 air km NW of Stinkingwater Peak, grassy alpine slopes, T55N R108W sect. 26, 3017–3078 m, 22 Jul 1985, *Hartman* 21376.
- Saxifraga rivularis* L. ssp. *rivularis* var. *flexuosa* (Sternb.) Engl. & Irmscher (Saxifragaceae).—Park Co., Sylvan Pass to Top Notch Peak, spruce–fir and whitebark pine forests and bald summits and rock outcrops, T52N R110W sect. 19, 20, 29, 30, 2651–3108 m, 29 Jun 1987, *Hartman and Snow* 23566.
- NEIL SNOW, B. E. NELSON, and RONALD L. HARTMAN, Rocky Mountain Herbarium, Department of Botany, University of Wyoming, Laramie, WY 82071-3165. (Received 4 Jan 1990; revision accepted 21 Feb 1990.)

---

## NOTEWORTHY COLLECTIONS

### ARIZONA

*CATHESTECUM ERECTUM* Vasey and Hack (GRAMINEAE).—Pima Co., Ragged Top, ca. 6.5 km N of Silver Bell, South slope of foothills 1 km ENE of Wolcott Peak, T11S R8E sect. 25 NE¼ & sect. 30 NW¼, 760 m, in silty clay soil among high-feldspar quartzite rubble, occasional in some areas, but dense with relatively continuous populations up to a hectare in others, with *Encelia farinosa*, *Carnegiea gigantea*, and *Hibiscus denudatus*, 25 Oct 1989, *J. F. Wiens* 89-RT-41 (ARIZ), determined by J. R. Reeder, 17 Nov 1989, *J. F. Wiens* 89-RT-44 (ASU, ASDM).

*Previous knowledge.* Known from NC-Sonora, E to Trans-Pecos Texas, S through much of Mexico, Guatamala, and El Salvador (Swallen, J. R., The grass genus *Cathestecum*. *J. Washington Acad. Sci.*, 1937, 27495–27501). Common on dry, rocky hills and plains in tropical and subtropical communities, and expected for Arizona (Gould, F. W., *Grasses of Southwestern United States*, Univ. Arizona Press, 1951, p. 154). Single Arizona collection by E. Palmer in 1869 (unnumbered at US) is labeled “southern Arizona”. Northernmost Sonoran localities are 25 km S of Pitiquito (1932,



*F. Shreve, 6020, ARIZ*), and Cinta de Plata (=Sierra Babiso), 27 km SE of Magdalena, (T. R. and R. K. Van Devender, obs. 1983, pers. comm. 1989).

*Significance.* This the first verified Arizona population; a range extension of ca. 225 km NNE of the Pitiquito collection, and ca. 225 km NNW of the Cinta de Plata sighting. Arizona occurrence is listed in most references as "southern Arizona (?)". The 1869 Palmer collection was made just 16 years after the Gadsen Purchase realigned the Arizona–Sonora boundary, and six years after the Arizona Territory was separated from New Mexico Territory, contributing to the vagueness and doubt regarding Arizona.

*PISONIA CAPITATA* (S. Wats) Standley (NYCTAGINACEAE).—Pima Co., Ragged Top, ca. 6.5 km N of Silver Bell, T11S R8E sect. 25 SW¼, 975 m, in silty soil in rhyolite substrate, with *Celtis pallida*, *Justicia californica*, and *Ambrosia ambrosioides*, 27 Mar 1989, *J. F. Wiens 89-RT-20* (ARIZ), determined by P. Jenkins, 24 Sept 1989, *J. F. Wiens 89-RT-37* (ASDM), 11 Nov 1989, *J. F. Wiens et al. 89-RT-43* (ASU).

*Previous knowledge.* Known from C Sonora to Tepic, Nayarit, Mexico (Standley, P. C., Contr. U.S. Natl. Herb. 13:388–389, 1912). Herbarium search revealed northern-most Sonoran specimens from San Carlos Bay, near Guaymas, on the Gulf of California, and from 20 km S of Soyopa, Sonora (1971, *R. M. Turner et al. 71–91*, ARIZ). Found in tropical deciduous forest along the Río Yaqui, Sinaloan thornscrub, and Sinaloan riparian gallery communities along river terraces and washes.

*Significance.* First record for this genus and species in Arizona, and for the species in the United States; a range extension of ca. 460 km NNW from the Soyopa locality. The microhabitat on Ragged Top is the S-facing wall of the canyon, within a cleft measuring 30 m deep (horizontally), and 7 m wide, with vertical sides 35 m tall. In the cleft all plants are etiolated to some degree from lack of light. One female *Pisonia capitata* measuring 1.5 m tall and 7 m wide covers a pocket of soil in the center of the site. Within its canopy are three small plants of undetermined sex. It appears that these may originate from branches of the larger plant which contacted the soil, rooted, and were subsequently buried by soil deposition. If so, this vegetative cloning would be an unusual character for the family (though known in *Bougainvillea*). A fifth plant, also female is in a disjunct soil pocket 9 m from the main plant. The female plants flower, but no seed set has been noted. If the three plants suggested to be clones are, in fact, that, then this group of plants would be reproductively sterile. The isolated northern occurrence of this tropical plant is probably due to transportation of the glandular fruit by a bird, and considered a freak dispersal rather than an indication of a former continuous population.—JOHN F. WIENS, 16920 W. Placita Mañana, Marana, AZ 85653.

#### MEXICO

*Chandonanthus hirtellus* (Fried. Weber) Mitten (Hepaticopsida: Jungermanniaceae).—Chihuahua. 17 mi E of Basaseachic on rd to Tomochic; ca. 108°01'W, 28°ca.15'N, elev. ca. 2400 m. Shaded cliff face beneath *Quercus* shrub, *Pinus–Quercus–Pseudotsuga* forest along a river, 3 Oct 1986. *A. T. Whittemore et al. 2839* (MEXU, PRC) (verified by J. Vana, PRC).

*Previous knowledge.* Widespread in southern and eastern Asia; in the New World known only from the Queen Charlotte Islands, British Columbia (W. B. Schofield, *J. Hattori Bot. Lab.* 31:272. 1968).

*Significance.* The first collection at low latitudes in the New World, representing a range extension of ca. 3500 km.

*Hypnum vaucherii* Lesq. (Bryopsida: Hypnaceae).—Coahuila–Nuevo Leon border. Ridge of Sierra La Marta, saddle immediately E of Cerro Morro, ca. 23 km (by air) ESE of San Antonio de las Alazanas; 100°22'W, 25°12'N, elev. 3600 m. Around crack



in rock face on crest of ridge in *Senecio-Lupinus*-grass herbland, 22 Jul 1985. *A. T. Whitemore et al.* 2647 (MEXU).

*Previous knowledge.* Circumboreal, S in western North America to Arizona and Colorado (Ando, J. Sci. Hiroshima Univ., Ser. B., Div. 2, Bot. 16:7–22. 1976).

*Significance.* New to Mexico.

*Omphalanthus wallisii* (Jack & Stephani) Gradst. (Hepaticopsida: Lejeuneaceae).—Chiapas. Disturbed cloud forest 5.5 mi SW of Motozintla on road to Huixtla; 92°ca. 17'W, 15°ca.20'N, elev. ca. 1800 m. On bark of trees, with *Dichaea*, 6 Jan 1984. *S. Sundberg et al.* s.n. (CAS, MEXU, NY) (verified by B. M. Thiers, NY); forming clumps on high NW-facing roadbank, same location and date. *A. T. Whitemore et al.* 2191 (MEXU, MO).

*Previous knowledge.* Colombia (Stephani, Species Hepaticarum 4:699, Geneva, 1911, as *Peltolejeunea wallisii* Jack & Steph.).

*Significance.* New to North America.

*Rhynchostegiopsis planifolia* H. Crum & E. Bartram (Bryopsida: Hookeriaceae).—Oaxaca. 31.4 mi S of Valle Nacional on hwy. 175; 96°ca.30'W, 17°ca.34'N, elev. ca. 3000 m. Shaded bank beneath bamboo on damp vertical roadbank, cloud forest with *Pinus*, 24 Aug 1982. *A. T. Whitemore 1889A with M. Leidig* (MEXU, MO) (verified by B. Allen, MO).

*Previous knowledge.* Known only from Jamaica (Crum & Bartram, Bull. Inst. Jamaica Sci. Ser. 8:55–56. 1958).

*Significance.* New to Mexico.—A. T. WHITEMORE, Dept. of Biology, Campus Box 1137, Washington University, St. Louis, MO 63130.

## ANNOUNCEMENT

### SEVENTH WILDLAND SHRUB SYMPOSIUM

The Shrub Research Consortium is sponsoring the Seventh Wildland Shrub Symposium 29–31 May 1991 at the Sun Valley Lodge/Inn, Sun Valley, Idaho. The symposium will address the biology and management of shrubs in riparian zones and other aspects of shrublands. A field trip is planned to view a variety of mountain meadow riparian areas. Contributed papers of 20 minutes duration are invited. The proceedings will be published by the USDA Forest Service, Intermountain Research Station.

If you would like to present a paper, send a title and abstract by 15 Dec 1990 to: Shrub Research Consortium, W. P. Clary, Forest Sciences Laboratory, 316 East Myrtle Street, Boise, ID 83702.

To receive preregistration materials and information please contact: Nancy Ness, Division of Continuing Education, Boise State University, 1910 University Drive, Boise, ID 83725.



## REVIEW

*Intermountain Flora: Vascular Plants of the Intermountain West, U.S.A.* By ARTHUR CRONQUIST, ARTHUR H. HOLMGREN, NOEL H. HOLMGREN, JAMES L. REVEAL, and PATRICIA K. HOLMGREN. Volume 3, Part B by RUPERT C. BARNEBY. The New York Botanical Garden, New York. 1989. ix + 279 pp., illustrated, endpaper maps. \$61.65 (U.S.), \$63.20 (non U.S.). ISBN 0-89327-346-5.

The fourth volume to appear in this series treats the Fabales. It is authored by Rupert C. Barneby, except for the genera *Pediomelum* and *Psoralidium* by James W. Grimes. It follows the format of preceding volumes and includes synonymy, description, common name, chromosome number, distribution, discussion of relationships, and illustrations of each taxon. Three families (as per Cronquist's interpretation), 33 genera, and 286 species are treated. Additionally 13 cultivated genera are characterized and included in the generic keys. Twenty-seven nomenclatural innovations are listed on the last page of the text. About one-third of the illustrations, by Jeanne R. Janish, are reproduced from Vol. 3, *Vascular Plants of the Pacific Northwest* (Hitchcock et al. 1961); new illustrations are by Bobbi Angell.

In evaluating a volume of this scope one should consider the usability of the keys, completeness and accuracy of descriptions and illustrations and their clarification of key characters. In general the keys are fairly easy to follow, but occasionally require some amplification of terminology and reference to illustrations. I found this particularly true for couplet 40 in the key to genera of Fabaceae. This couplet separates *Astragalus* and *Oxytropis* with the following lead:

- 40 Blades of keel-petals incurved to an obtusely rounded, deltate, or triangular apex, this situated asymmetrically on the blade's adaxial side [. . .] . . . . . *Astragalus*  
40 Blades of keel-petals abruptly contracted just below the true apex into an erect or recurving, conic or subulate beak situated terminally or slightly to the abaxial side of the blade [. . .] . . . . . *Oxytropis*

The illustrations do not serve to clarify these leads. Excised keels are illustrated in only two taxa (*A. miser* Douglas ex Hook. on p. 65 and *A. tiehmii* Barneby on p. 167), and the flower illustrations of just three *Oxytropis* taxa show the keel. The feature is clarified somewhat in the description of *Oxytropis*: "keel abruptly contracted at apex into an erect or recurved, subulate beak or conical point". It seems to me that the second quote would be more reasonable wording for a key, and that illustrations should have been designed to show the difference.

In contrast to couplet 40, Barneby explains on p. 40 that close observation and care are needed to distinguish some technical characters in *Astragalus*. He explains how to distinguish cauline, adnate and connate stipules, dolabriform and basifixed hairs, stipe and gynophore. Many illustrations show the stipule features, and stipe or gynophore are clearly illustrated where necessary. Since the 156 species and 122 varieties of *Astragalus* account for over 50% of Intermountain Fabales, the explanation and illustrations are very helpful.

The 27 nomenclatural innovations include two species (*Astragalus welshii* Barneby and *Lathyrus grimesii* Barneby), six varieties, and 19 varietal combinations. Eleven new combinations are in four species of perennial *Lupinus*, and seven of these are for *L. argenteus* Pursh.

The small flowered lupines are a notoriously difficult group that has been overly fractured by previous workers. Barneby's treatment of *L. argenteus* with 13 varieties is (p. 248) "a logical extension southward of that proposed by Hitchcock" (in Hitchcock et al. loc. cit.). About 100 names including *L. alpestris* A. Nels., *L. caudatus*



Kellogg, *L. hillii* Greene, *L. holosericeus* Nutt. ex Torr. & Gray, *L. montigenus* A. A. Heller, and *L. meionanthus* A. Gray are synonymized. While some might regard this treatment as overly conservative, I think it is more realistic. Barneby rightly criticizes the ad hoc hypotheses that have been advanced to explain variation and evolution in the group. In his discussion of *L. arbustus* Douglas ex Lindl., he notes that, outside the Intermountain area, variants with short spurred calyces or lacking the patch of hairs on the wings (the latter as illustrated, by the way) grade into *L. argenteus*. He suggests that if *L. arbustus* were lumped with *L. argenteus*, one would see a closed circle of variation and affinity. Should the suggestion be formalized, a morass of west American lupines would be reduced to one highly, highly variable taxon. Perhaps such a move would result in the proper burial of some outlandish tales that accompany *Lupinus*!

Barneby also chooses a conservative treatment of the dwarf or caespitose lupines which exhibit continuous and independent variation in quantitative characters used by previous authors. Hitchcock's 1961 treatment of *L. lepidus* Douglas is expanded and some California taxa are submerged. *Lupinus sellulus* Kellogg is reduced to *L. lepidus* var. *sellulus* (Kellogg) Barneby; *L. culbertsonii* Greene is *L. l.* var. *culbertsonii* (Greene) C. P. Smith; *L. confertus* Kellogg is *L. l.* var. *confertus* (Kellogg) C. P. Smith, and *L. hypolasius* Greene is synonymous with *L. l.* var. *ramosus* Jepson. In what appears to be a liberal treatment of the Sierran tufted lupines, *L. tegeticulatus* Eastw. is segregated from *L. breweri* A. Gray. But Barneby's evaluation is obvious; *L. tegeticulatus* is defined as obligately acaulescent and having an above ground caudex, whereas *L. breweri* is caulescent and has a subterranean caudex.

Barneby's overhaul of *Lupinus* does not extend to the annual species, but several are centered in California outside the Intermountain region. With exception of *L. odoratus* A. A. Heller, most annual lupines of the Mojave Desert could be identified with his keys. California specimens of *L. odoratus* usually have an upper calyx lip more, not less, than one-half as long as the lower.

Two other taxonomic opinions by Barneby should be mentioned because they pertain to taxa widely distributed in the Western U.S. In both cases he argues against dispersal [distribution] as a defensible criterion for species recognition especially if morphological features are not concordant. Thus the western redbud becomes *Cercis canadensis* L. var. *orbiculata* (Greene) Barneby, whereas *C. occidentalis* Torr. ex A. Gray is referred to *C. c.* var. *texensis*. (S. Wats.) M. Hopk. In the second case he concludes that all western *Thermopsis* should be referred to the megaspecies *T. rhombifolia* (Nutt. ex Pursh) Richardson, but extralimital *T. macrophylla* H. & A. is not listed in synonymy.

Rupert Barneby's previous publications in legumes are regarded as landmark works, and this volume is no exception. Perhaps some key leads and illustrations could have been clearer, but neither detract from the overall quality of the work. It should, and will I think, be a major reference for North American legumes for many years to come. Everyone interested in western American plants, and legumes in particular, should add this volume to his or her library. — RHONDA RIGGINS, Biological Sciences Department, California Polytechnic State University, San Luis Obispo, CA 93407.



## MEMORIAL

WILLIAM BURKE CRITCHFIELD  
(1923–1989)

William B. Critchfield died 11 July 1989. He left a legacy unparalleled in forest genetics. Bill made major contributions to understanding genetic variation, hybridization, growth and development, biogeography, paleobotany, systematics, and taxonomy of forest trees, especially pines. In each of these fields, Bill's pioneering work earned him the position of world authority. These studies were mainly spinoffs from groundwork Bill was meticulously laying for his primary interest: unraveling the evolutionary history of conifers. And it is his evolutionary syntheses that best reveal Bill's breadth as geneticist and scholar.

Bill was born 21 November 1923 in Minneapolis, Minnesota, but grew up in North Dakota where his father had been among the state's pioneering settlers. He attended North Dakota Agricultural College (now North Dakota State University) before serving in the Navy during World War II. Upon returning from the South Pacific, he entered the University of California at Berkeley, where he completed his bachelor's degree with honors in Forestry in 1949 and his doctorate in Botany under Herbert Mason in 1956.

Bill's first position after receiving his doctorate was at Harvard University, where he worked from 1956–1959 as Geneticist with the Maria Moors Cabot Foundation for Botanical Research. In 1959 he moved back to Berkeley, California to join the Pacific Southwest Forest and Range Experiment Station of the U.S. Forest Service. He divided his time for the next 28 years between his office in Berkeley and the herbaria and arboreta of the Institute of Forest Genetics in Placerville. In 1972 he was appointed a Pioneering Research Scientist, an honor reserved by the Forest Service to promote the work of its most outstanding scientists. As one of only seven pioneering scientists in the agency, Bill was given carte blanche to pursue research of his own choice and design.

Bill's inferences about conifer evolution were grounded in an intimate knowledge of genecological variation. His early work on geographic variation and subspecific differentiation in lodgepole pine was seminal. He observed and measured morphological, physiological, and biochemical variation, and its relation to the environment in western conifers. He was convinced of the importance of studying species in their natural habitat, despite difficulties of access. In his studies of lodgepole pine in the 1950's, for example, he traveled the range of the species from California to Canada to Colorado by public buses, setting off from remote terminals to reach his forest destination on foot. He was alone on one collecting trip in British Columbia when he fell out of a tree, broke his back, and had to crawl to a road for help.

When Bill first joined the Forest Service, the Institute of Forest Genetics was engaged full-swing in a program of interspecific hybridization. Pine hybrids were being produced en masse and tested for their use in forestry and tree breeding. Jack Duffield, who had been at the Institute from about 1945–1955 had begun to use crossability as a measure of phylogenetic relationship among taxa. Bill continued this work with his own program of hybridization among pines and firs. Bill was unrelenting in his demand for experimental controls in this work. He insisted that only crosses using the same seed parent were comparable, and he was not willing to measure crossability by accepting the convention of counting the number of cones or seeds produced after artificial pollinations. He insisted instead on growing progeny in the nursery to confirm or reject their hybrid condition himself.

Bill soon became the leading authority on interspecific hybridization of pines. In



publications from 1963 to 1988, he shed light on hybridization and evolutionary relationships among almost all the subsections of *Pinus*, including the southern and western yellow pines, *Contortae*, *Sylvestres*, the California big-cone and closed-cone pines, the foxtail pines, and the white pines. He even studied hybridization among the western firs.

Bill's quest to determine evolutionary relationships among pines led him also to study their biogeography. Bill became the world's foremost authority on the geographical distribution of pines, and, with Elbert Little, he published a monumental book of maps that detailed ranges of every pine species. This book may well be the most widely cited reference in forestry. At a regional level, Bill undertook the enormous task of mapping all 86 tree species in California. In this book, Bill and coauthor Jim Griffin mapped the species in great detail, including both major and minor populations of the species, and even stands of only a few trees. For anyone who has relied on finding disjunct or tiny stands of California trees, Bill's map book is meticulous in its accuracy. The availability of such detailed information has allowed a standard of accuracy unprecedented elsewhere. These books are widely used references in many fields in addition to forestry, and although they were published years ago, they are still being requested.

Bill was a world authority on pine systematics and taxonomy. Since pines were first scientifically described by Linnaeus in 1753, over 40 classification systems have appeared. Of these, George Russell Shaw's evolutionary treatment of pine classification in 1914 set a new standard. With Elbert Little, Bill continued in the line of Shaw, and published a revised evolutionary classification of pines in 1966 and 1969. This system incorporated modern information on genetic variation in pines and on evolutionary relationships based on pine hybridization work. Furthermore, Critchfield and Little brought the nomenclature of the genus up to botanical code, an awesome task because invalid Latin names for pines proliferate wildly in the literature.

Critchfield and Little's classification stands as the accepted authority for pines. New species that have been discovered since its publication corroborate the classification. Bill became the world authority in identifying pine species, and he spent many hours with razor blades and dissecting scope making identifications for colleagues. Bill's botanical training amply prepared him for investigations of anatomy, and he had lifelong interests in morphology and ontogeny as subjects in themselves.

In later years, Bill realized that only when genetic information is combined with the paleohistoric record can present phylogenetic relationships of taxa be elucidated. This came as a personal revelation to Bill, and he would shake his head in amazement when he recounted how the thought of taking a course in paleobotany as a graduate student in evolution never occurred to him.

Bill more than made up for that lack in his past during his last ten years. With unbridled enthusiasm, he dissected the literature on the Quaternary history of North American conifers, and in case after case, made sense of anomalous patterns of genetic variation by documenting historic migrations and refugia. His seminal papers on this topic, culminating in "Impact of the Pleistocene on North American Conifers", were ahead of their time, with implications still not fully appreciated by the scientific community. He had begun work on similar topics for Japan and western Europe that unfortunately he will be unable to write.

Bill's scientific contributions went far beyond the professional papers he published and lectures he presented. He devoted long hours to related botanical efforts. At the Institute of Forest Genetics in Placerville, he reorganized and expanded the collection of herbarium specimens into what is probably the most complete pine herbarium in the world<sup>1</sup>. To the National Forest System of the Forest Service, he contributed much of his time promoting the Research Natural Areas program, a system of ecological reserves that protects representative vegetation communities of the region. And when

<sup>1</sup> The herbarium was recently named the William B. Critchfield Conifer Herbarium in his honor.



the California Native Plant Society was first documenting the extent of rare and endangered plants in California, Bill was a major contributor.

The many scientists who were peers or apprentices of Bill remember him as much for how he conducted science as for his accomplishments. Bill was foremost a scholar. He was relentlessly thorough and devastatingly honest. His literature searches left no lead untraced; his reviews of manuscripts were incisive. Once when he was showing me around the basement of the Institute of Forest Genetics, he pointed to a large collection of musty boxes containing cones from an old study. "I'm glad I kept those," he said, "because when I reviewed a manuscript recently, the author was building a shaky hypothesis that I wanted to test independently. I brought out all these old cones and measured them, and sure enough, the hypothesis didn't hold water." After his death, in poking through the herbarium, I came across an old note on a napkin from a colleague, in which he asked Bill a casual question about pine morphology. Bill's five-page typed reply, complete with references, was stapled to the napkin.

Bill was one of the best investments the Forest Service ever made, if for no other reason than the cost/benefit ratio was so high. He made his most significant contributions without recourse to highly technical equipment. His most sophisticated laboratory tool was a dissecting scope, and his annual supply budget consisted mostly of new packs of razor blades. His most well-honed tool was the language. He had a lifelong love affair with words. He treasured them, savored them, and used them with precision.

The epithet most often used for Bill in addition to scholar is mentor. Bill gave equally of his time and scholarship to others. Although he was never formally a professor or teacher, his professional judgement was sought by peers and students alike, but students especially would beat a path to his door, and he always received them. He had a warm and generous relationship with students, and was equally capable of being serious or frivolous with them. Completely missing from Bill was any formal facade or aloofness that drives students from seeking counsel of many established scientists. Bill loved his adventures with students, and he enjoyed as much as they did telling jokes on himself. Over the years, summer interns at the Institute of Forest Genetics developed nicknames for Bill, including "Critch", "Mr. Bill", and "Mr. Institute". These names show the range of feeling students felt for Bill, from endearment to profound respect.

Bill was the glue that held his colleagues together in the Forest Service. They gathered around him at coffee, they gravitated toward his raspy voice in the hall. He was the one who regularly gave parties for his colleagues at his small bachelor apartment in Berkeley. His hospitality was legendary, despite his grumbling about people "staying past 10 PM".

After his retirement from the Forest Service in early 1988, Bill set forest genetics aside. He had too much more to do. He had his lifelong loves of theater and mystery novels to indulge. And he had ambitions for many new pursuits. He began taking college courses in literature, history, and art; he was working on a world gazetteer of maps for famous crimes, fictional and real, at the time of his death. In his hobbies as well as his profession, Bill applied his characteristic thoroughness and honesty.

Bill had a bad heart. In 1974 and Christmas 1988 he had major heart attacks. A three-way bypass after his last attack gave the promise of many more productive years. On 11 July 1989, however, a sudden massive heart attack took his life. Critch died doing one of the things he loved best, attending theater in San Francisco.—  
CONNIE MILLAR, Institute of Forest Genetics, Berkeley, CA, with contributions from M. T. Conkle, B. B. Kinloch, R. M. Lanner, and F. T. Ledig.



## ANNOUNCEMENTS

## NEW PUBLICATIONS

MATHEW, BRIAN. *The genus Lewisia*. Royal Botanic Gardens, Kew, 1989, 151 pp., 20 pls. (color), text illus. (B&W), ISBN 0-88192-158-0 (hardbound), US\$29.95 (from Timber Press, 9999 SW Wilshire, Portland, OR 97225). [Publ. in Britain by Christopher Helm, 21-25 N. St., Bromley, Kent BR1 1SD, ISBN 0-7470-2217-8. = *A. Kew Magazine Monograph* (unnum.). Contents: intro.; history of *Lewisia* (Portulacaceae); history idem in cultivation; morphology; pollination and compatibility; cytology; conservation; cultivation (by K. Dryden); tax. (19 spp.); hybrids; cultivars; appendices (1 new subgen., 5 new sect.); dates publ. spp. and intro. into British cultivation; awards to *Lewisia*; biblio.; index; with nice illus. by Christabel King.]

TRIMBLE, STEPHEN. *The sagebrush ocean: a natural history of the Great Basin*. University of Nevada Press, Reno, NV 89557, 1989, xiv, 248 pp., 32 pls. (color), text illus. (B&W), ISBN 0-87417-128-8 (hardbound), \$34.95. [= *Max C. Fleischmann series in Great Basin natural history* (unnum.). Contents: the four Great Basins; making of a desert; relative reality of natural communities; paleobiogeography; mountains as islands; playas and salt deserts; shadscale; sagebrush; dunes; wetlands; piñon-juniper woodland; mountain brush and aspen glens; bristlecone pines and subalpine forest; tundra; west of the Wasatch; east of the Sierra; appendix (sci. names plants, animals); notes; biblio.; index. This oversize book (23.5 × 31.0) can be enjoyed on two levels: as a coffee table book, especially for the superb color photos by the author; as a scientific treatise, though the style of writing is more in the discursive naturalistic rather than tight biological mode.]

WATSON, L. and M. J. DALLWITZ. *Grass genera of the world—interactive identification and information retrieval*, 1989, a set of computer (MS/PC-DOS) data files for use with the DELTA system. [These files (see also *Taxon* 39:286 for the related booklet) are freely available for research purposes as issue 22 of Flora Online through TAXACOM, an electronic service for syst. biology, as well as by mail from L. Watson (Taxonomy Laboratory, Research School of Biological Sciences, G.P.O. Box 475, Canberra, ACT 2601). With the INTKEY program from the Dallwitz-Paine set of DELTA programs, the most recent versions of which are also available through TAXACOM from its DELTA Conference, morphological and geographic info. on all the grass genera worldwide may be used for computerized tax. identifications. An extensive bibliography is also included. Any interested person may call and download issue 22 by logging on to TAXACOM as a "GUEST." Contact is by asynchronous modem through standard telephone lines at (716) 896-7581, 300 or 1200 or 2400 bps, 8 data bits, no parity, one stop bit (users outside USA should note use of CCITT protocol at 2400 bps, but Bell protocols at 300 and 1200 bps). For more info. see *Taxon* 38:456 or contact Richard H. Zander, 1020 Buffalo Museum of Science, Buffalo, NY 14211, USA.—Richard H. Zander, BUF.]



## SUBSCRIPTIONS—MEMBERSHIP

Membership in the California Botanical Society is open to individuals (\$22 per year; students \$12 per year for a maximum of seven years). Members of the Society receive MADROÑO free. Family memberships (\$25) include one five-page publishing allotment and one journal. Emeritus rates are available from the Corresponding Secretary. Institutional subscriptions to MADROÑO are available (\$30). Membership is based on a calendar year only. Applications for membership (including dues), orders for subscriptions, and renewal payments should be sent to the Treasurer. Requests and rates for back issues, changes of address, and undelivered copies of MADROÑO should be sent to the Corresponding Secretary.

## INFORMATION FOR CONTRIBUTORS

Manuscripts submitted for publication in MADROÑO should be sent to the editor. All authors must be members, and membership is prerequisite for review.

Manuscripts may be submitted in English or Spanish. English-language manuscripts dealing with taxa or topics of Latin America and Spanish-language manuscripts must have a Spanish RESUMEN and an English ABSTRACT.

Manuscripts and review copies of illustrations must be submitted in triplicate for all articles and short items (NOTES, NOTEWORTHY COLLECTIONS, POINTS OF VIEW, etc.). Follow the format used in recent issues for the type of item submitted. Allow ample margins all around. Manuscripts MUST BE DOUBLE SPACED THROUGHOUT. For articles this includes title (all caps, centered), author names (all caps, centered), addresses (caps and lower case, centered), abstract and resumen, text, acknowledgments, literature cited, tables (caption on same page), and figure captions (grouped as consecutive paragraphs on one page). Order parts in the sequence listed, ending with figures. Each page should have a running header that includes the name(s) of the author(s), a shortened title, and the page number. Do not use a separate cover page or “erasable” paper. Avoid footnotes except to indicate address changes. Table and figure captions should contain all information relevant to information presented. All measurements and elevations should be in metric units. Specimen citations may include English or metric distance measurements.

Line copy illustrations should be clean and legible, proportioned (including captions) to the MADROÑO page, and designed for reduction to  $\frac{2}{3}$  original size. Scales should be included in figures, as should explanation of symbols, including graph coordinates. Symbols smaller than 1 mm after reduction are not acceptable. Maps must include latitude and longitude references. Halftone copy should be designed for reproduction at actual size. In no case should original illustrations be sent prior to the acceptance of a manuscript. When needed they should be mounted on stiff cardboard and sent flat. No illustrations larger than 22 × 28 cm will be accepted.

Presentation of nomenclatural matter (accepted names, synonyms, typification) should follow the format used for members of the *Allium sanbornii* complex in MADROÑO 36:124–128. 1989. Institutional abbreviations in specimen citations should follow Holmgren, Keuken, and Schofield, *Index Herbariorum*, 7th ed. Names of authors of scientific names should be abbreviated according to the Kew *Draft Index of Author Abbreviations* (1980). Abbreviation of serial titles should be those in *Botanico-Periodicum-Huntianum* (Lawrence et al., 1968, Hunt Botanical Library, Pittsburgh). If the correct abbreviation cannot be determined, the full serial title should be used. Titles of books should be given in full, together with the place and date of publication, publisher, and edition, if other than the first.

All members of the California Botanical Society are allotted five free pages per volume in MADROÑO. Joint authors may split the full page number. Beyond that number of pages a required editorial fee of \$65.00 per page will be assessed. The purpose of this fee is not to pay directly for the costs of publishing any particular paper, but rather to allow the Society to continue publishing MADROÑO on a reasonable schedule, with equity among all members for access to its pages. Printer's fees for illustrations and typographically difficult material @ \$35.00 per page (if their sum exceeds 30 percent of the paper) and for author's changes after typesetting @ \$4.50 per line will be charged to authors.

At the time of submission, authors must provide information describing the extent to which data in the manuscript have been used in other papers that are published, in press, submitted, or soon to be submitted elsewhere.





CALIFORNIA BOTANICAL SOCIETY



QK  
-  
M183  
Bot.

## MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

## Contents

|  |     |
|--|-----|
| GROWTH DYNAMICS OF TWO CHAPARRAL SHRUB SPECIES WITH TIME AFTER FIRE<br><i>Anne Larigauderie, Terry W. Hubbard, and Jochen Kummerow</i>   | 225 |
| DEMOGRAPHIC STRUCTURE OF CALIFORNIA BLACK WALNUT ( <i>JUGLANS CALIFORNICA</i> ;<br>JUGLANDACEAE) WOODLANDS IN SOUTHERN CALIFORNIA<br><i>Jon E. Keeley</i>                              | 237 |
| HABITAT RELATIONSHIPS OF THE PACIFIC COAST SHRUB <i>OEMLERIA CERASIFORMIS</i><br>(ROSACEAE)<br><i>Joseph A. Antos and Geraldine A. Allen</i>   | 249 |
| DISTRIBUTION, ECOLOGY, AND TAXONOMY OF <i>ERYTHRONIUM</i> (LILIACEAE) IN THE SIERRA<br>NEVADA OF CALIFORNIA<br><i>James R. Shevock, Jim A. Bartel, and Geraldine A. Allen</i>          | 261 |
| CYTOLOGICAL, MORPHOLOGICAL, ECOLOGICAL AND PHENOLOGICAL SUPPORT FOR<br>SPECIFIC STATUS OF <i>CRATAEGUS SUKSDORFII</i> (ROSACEAE)<br><i>Steven J. Brunsfeld and Frederic D. Johnson</i> | 274 |
| <i>BERBERIS PIMANA</i> (BERBERIDACEAE): A NEW SPECIES FROM NORTHWESTERN MEXICO<br><i>Joseph E. Laferrière and Jorge S. Marroquín</i>   | 283 |
| A NEW <i>GENTIANA</i> (GENTIANACEAE) FROM NORTHERN CALIFORNIA AND SOUTHERN<br>OREGON<br><i>Charles T. Mason, Jr.</i>   | 289 |
| <i>THELESERMA CAESPITOSUM</i> (ASTERACEAE), A NEW SPECIES FROM WYOMING AND UTAH<br><i>Robert D. Dorn</i>   | 293 |
| A NEW SUBSPECIES OF <i>CIRSIIUM PARRYI</i> (ASTERACEAE: CARDUEAE) FROM ARIZONA AND<br>COMMENTS ON THE <i>CIRSIIUM PARRYI</i> COMPLEX<br><i>C. G. Schaack and Gregory A. Goodwin</i>    | 299 |
| A NEW SUBSPECIES OF <i>CLARKIA CONCINNA</i> (ONAGRACEAE) FROM MARIN COUNTY,<br>CALIFORNIA<br><i>G. A. Allen, V. S. Ford, and L. D. Gottlieb</i>  | 305 |
| NOTES  |     |
| HERBARIA OF NEW MEXICO<br><i>Carolyn Dodson</i>  | 311 |
| NOTEWORTHY COLLECTIONS   |     |
| MEXICO: BAJA CALIFORNIA SUR  | 236 |
| REVIEW   | 314 |
| ANNOUNCEMENTS  |     |
| NEW MADRONO EDITOR   | 282 |

(continued on back cover)



MADROÑO (ISSN 0024-9637) is published quarterly by the California Botanical Society, Inc., and is issued from the office of the Society, Herbarium, Life Sciences Building, University of California, Berkeley, CA 94720. Subscription rate: \$30 per calendar year. Subscription information on inside back cover. Established 1916. Second-class postage paid at Berkeley, CA, and additional mailing offices. Return requested. POSTMASTER: Send address changes to Mona Bourell, Botany Dept., California Academy of Sciences, San Francisco, CA 94118.

*Editor*—DAVID J. KEIL  
Biological Sciences Department  
California Polytechnic State University  
San Luis Obispo, CA 93407

*Board of Editors*

Class of:

- 1990—STEVEN TIMBROOK, Ganna Walska Lotusland Foundation, Montecito, CA  
THOMAS R. VAN DEVENDER, Arizona-Sonora Desert Museum, Tucson, AZ  
1991—JAMES HENRICKSON, California State University, Los Angeles, CA  
WAYNE R. FERREN, JR., University of California, Santa Barbara, CA  
1992—BRUCE A. STEIN, The Nature Conservancy, Washington, D.C.  
WILLIAM L. HALVORSON, Channel Islands National Park, Ventura, CA  
1993—JON E. KEELEY, Occidental College, Los Angeles, CA  
RHONDA L. RIGGINS, California Polytechnic State University, San Luis Obispo, CA  
1994—BRUCE D. PARFITT, Arizona State University, Tempe, AZ  
PAUL H. ZEDLER, San Diego State University, San Diego, CA

---

CALIFORNIA BOTANICAL SOCIETY, INC.

OFFICERS FOR 1990-91

- President:* THOMAS DUNCAN, University Herbarium, University of California, Berkeley, CA 94720  
*First Vice President:* MARY ANN T. SHOWERS, California Department of Parks and Recreation, Sacramento, CA 94296  
*Second Vice President:* LOREN RIESEBERG, Rancho Santa Ana Botanic Garden, Claremont, CA 91711  
*Recording Secretary:* NIALL MCCARTEN, Department of Integrative Biology, University of California, Berkeley, CA 94720  
*Corresponding Secretary:* BARBARA ERTTER, University Herbarium, University of California, Berkeley, CA 94720  
*Treasurer:* MONA BOURELL, Department of Botany, California Academy of Science, San Francisco, CA 94118  
*Financial Officer:* BARRETT ANDERSON, EIP California, San Francisco, CA 94107

The Council of the California Botanical Society consists of the officers listed above plus the immediate *Past President*, ROBERT W. PATTERSON, Biological Sciences Department, San Francisco State University, San Francisco, CA 94132; the *Editor* of MADROÑO; three elected *Council Members*: DAVID A. YOUNG, Santa Barbara Botanic Garden, Santa Barbara, CA 93105; ELIZABETH MCCLINTOCK, University Herbarium, University of California, Berkeley, CA 94720; BARBARA PITSCHER, Strybing Arboretum, Golden Gate Park, San Francisco, CA 94118; and a *Graduate Student Representative*.

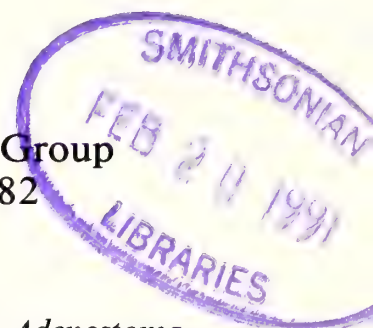
|   |
|---|
| THIS PUBLICATION IS PRINTED ON ACID-FREE PAPER. |
|---|



# GROWTH DYNAMICS OF TWO CHAPARRAL SHRUB SPECIES WITH TIME AFTER FIRE

ANNE LARIGAUDERIE, TERRY W. HUBBARD,  
AND JOCHEN KUMMEROW

Biology Department and Systems Ecology Research Group  
San Diego State University, San Diego, CA 92182



## ABSTRACT

The effect of stand age on growth dynamics of two chaparral shrubs, *Adenostoma fasciculatum* and *Ceanothus greggii*, was studied in southern California. It was asked whether shoots of young shrubs grow faster than those of old ones, and if on young shrubs more shoots develop per square meter of canopy projection area than on old ones. These measurements were made in ten chaparral stands representing six different ages ranging from 6 to 87 years. Measurements taken biweekly throughout the 1984 growing season indicated no decline in growth rates or biomass of new shoots with increasing stand age. Variability in measurements was as high among even-aged stands as among stands of differing ages. Measured values were very low compared to earlier studies, probably because of very low rainfall in 1983–1984.

It has often been assumed that chaparral shrubs become senescent in the long absence of fire (Hanes 1971; Parsons 1976; Rundel and Parsons 1979, 1980). Recent reviews, however, have concluded that there is no clear evidence in favor or against a decline (*sensu* Noodén 1988) at the shrub level in chaparral (Zedler and Zammit 1989; Hilbert and Larigauderie 1990). Two studies using different approaches have focussed on the possibility of a decline with time after fire. A demographic study of even-aged stands of *Ceanothus megacarpus* by Montygiard-Loyba and Keeley (1987) suggested that shrub mortality between 8 and 55 years after fire is related more to intra-specific competition than to shrub decline. Mortality appeared to be more frequent in smaller plants. A study of *Adenostoma fasciculatum* by Rundel and Parsons (1979) showed that in stands older than 60 years, shrub size and leaf area index were reduced compared to shrubs found in younger stands, suggesting a decline of this shrub with age.

The goal of our study was to assess the effect of stand age on growth dynamics of two chaparral shrubs, *Adenostoma fasciculatum*, a resprouter, and *Ceanothus greggii*, an obligate seeder. A common assumption in California chaparral is that *C. greggii* is shorter-lived than *A. fasciculatum* and dies within 30 to 40 years after fire (Keeley 1975). There is, however, only limited support for this assumption. Zammit and Zedler (*pers. comm.*) found that the number of *C. greggii* shrubs per ha declined with increasing stand age, but Keeley



TABLE 1. LOCATION, YEARS SINCE THE LAST FIRE, ELEVATION, PRECIPITATION (FROM OCTOBER 1983 TO APRIL 1984), AND SOIL TYPES FOR THE 10 CALIFORNIA CHAPARRAL STANDS. All stands were on north-facing slopes.

| Stand age<br>(in years<br>since fire) | Location       | Elevation<br>(m) | Precipitation<br>(mm) | Soil      |
|---------------------------------------|----------------|------------------|-----------------------|-----------|
| 6                                     | Warner Springs | 1091             | 113                   | Sheephead |
| 13a                                   | Warner Springs | 1164             | 113                   | Sheephead |
| 13b                                   | Warner Springs | 1285             | 113                   | Sheephead |
| 13c                                   | Warner Springs | 1285             | 113                   | Sheephead |
| 32                                    | Warner Springs | 1150             | 113                   | Sheephead |
| 56a                                   | Warner Springs | 1188             | 113                   | Sheephead |
| 56b                                   | Sky Oaks       | 1408             | 292                   | Tollhouse |
| 56c                                   | Sky Oaks       | 1552             | 292                   | Sheephead |
| 82                                    | Warner Springs | 1006             | 113                   | Sheephead |
| 87                                    | Sky Oaks       | 1415             | 292                   | Sheephead |

(1975) documented that *C. greggii* can be an important part of chaparral even 90 years after fire. We expect shoot growth rate and shoot biomass production per m<sup>2</sup> projected canopy area to be a measure of general shrub vigor, and hypothesize that if decline is taking place with age, these variables will be lower in old than in young shrubs. Such a decline should occur especially in *C. greggii* if it is shorter-lived than *A. fasciculatum*.

#### STUDY SITES

Chaparral stands that had not burned for 6, 13, 32, 56, 82, or 87 years were used for the measurements. The number of years since the last fire will be referred to as the age of the stand hereafter. The 13 and 56 year old stands had three replicates whereas the other ages were represented by one stand each. Two 56 (b and c) stands and the 87 year old stand were situated at the Sky Oaks Biological Field Station, and will be referred to as the Sky Oak stands. The seven other stands were in the Cleveland National Forest adjacent to the biological field station and are referred to as Warner Springs stands. The Sky Oaks field station is situated 15 km northeast of Warner Springs, which is approximately 70 km northeast of San Diego, California. All stands grew on north facing slopes. The main stand characteristics are presented in Table 1. Nine stands occurred on the Sheephead soil series, a loamy, mixed, mesic, shallow Ultic Haploxeroll, and one stand occurred on the Tollhouse soil series, a loamy, mixed, mesic, shallow Entic Haploxeroll. The maximum and minimum distance between two stands was approximately 11 and 1.5 km, respectively. This close proximity minimized possible differences among stands due to precipitation.



## METHODS

*Stand age.* A main stem from six randomly selected shrubs of each species was sawed off close to the ground in each of the stands and the stem base was taken to the laboratory. Cross sections from the stem bases were sanded and polished prior to year ring counting. In each stand the stem with most year rings was used to decide on the age of the stand. Incomplete rings were considered false rings and were not counted.

*Shoot growth.* Shoot growth was monitored throughout the 1984 growing season. *Adenostoma fasciculatum* forms new tissue on short and long shoots. Short shoots are borne on both current year's long shoots and on stems produced prior to the current season. All short shoots contribute annually to leaf production (Jow et al. 1980). In the present study we measured long shoots with their attached short shoots only. Prior to growth initiation, twelve *A. fasciculatum* and twelve *C. greggii* shrubs were randomly selected in each of the ten stands. Only four and six shrubs could be selected in the 82 and 87 year old stand, respectively, because of the limited number of *C. greggii* shrubs in these old stands. At the time of shrub selection six randomly chosen branches on each shrub were flagged.

Once spring growth began, the lengths of the developing shoots were measured at two to three week intervals. Shoot length measurements were made throughout the growing season, the end of which was defined as the time when two consecutive measurement periods did not yield any additional growth.

Final shoot lengths were used to calculate average shoot growth rates (presented in Fig. 2) based on the number of days during which at least six shoots were growing in the stand.

*Shoot biomass production.* The total biomass of new (1984) shoots per m<sup>2</sup> projected canopy area was estimated at the end of the growing season for the same shrubs that were used to measure growth rates, using a sample branch method described in Mooney and Kummerow (1977). Leaves of chaparral shrubs generally grow at the distal 30 cm of each branch; therefore a sample branch consisted of the distal 30 cm of a foliated branch. Lateral shoots attached to the main axis were included as part of the sample branch. The total number of sample branches was counted on each shrub. A branch segment with leaves beyond the distal 30 cm was counted as another sample branch. Sample branches per shrub were counted by two observers. The counting was repeated when discrepancies exceeded 5 percent of the mean of the two counts. Projected canopy area for each shrub was assumed to be equal to the area of a circle calculated by using the mean diameter of each shrub. This value was the result of three diameter measurements.



Twelve sample branches were harvested from each shrub. In order to collect these sample branches in an unbiased fashion, the shrub circumference was divided into twelve sectors. One of the twelve sectors was chosen by means of a random number. A second random number was used to indicate height above the ground. The sample branch closest to these two coordinates was harvested. The sample branches were separated into 1984 shoots, including stems, leaves, and flowers, and 1983 and older leaves and stems. Dry weights of each fraction were recorded for the individual sample branches (drying during 72 hr at 78°C).

Dry weight of the 1984 tissues of the mean sample branch (mean of 12 individual branches) was multiplied by the number of sample branches per m<sup>2</sup> of canopy projection.

## RESULTS

*Precipitation.* Monthly precipitation for 1983–1984 is presented in Fig. 1. Seasonal rainfall (October to April) for the growing season 1983–1984 was 292 and 113 mm at Sky Oaks and Warner Springs, respectively.

*Shoot growth rates.* The long shoots of *A. fasciculatum* grew between 0.2 and 0.7 mm/day and those of *C. greggii* between 0.1 and 0.25 mm/day (Fig. 2). The slopes of the regression lines for mean shoot growth rates versus stand age were not significantly different from zero for either shrub species studied ( $p > 0.1$  for both species).

*Shoot elongation.* *Ceanothus greggii* shrubs in the three stands at Sky Oaks and the 32 year old stand at Warner Springs initiated growth in mid-March, later than the other six stands in the study (Fig. 3). In two of the three Sky Oaks stands (56c, 87), *A. fasciculatum* shrubs exhibited delayed growth initiation similar to the trend observed in *C. greggii* (Fig. 3). *Adenostoma fasciculatum* shrubs in the remaining Sky Oaks stand (56b) however, initiated growth concurrently with shrubs in stands at Warner Springs and continued to grow through June 16 when growth of all other shrubs had ceased.

Total new shoot length throughout the 1984 growing season varied between 2 and 22 mm for *C. greggii* and 8 and 65 mm for *A. fasciculatum* in the various stands. Shoot length was not correlated with stand age.

*Shoot biomass production per shrub.* The highest new shoot production in both species (48.5 and 26.7 g/m<sup>2</sup> projected canopy area for *C. greggii* and *A. fasciculatum*, respectively) occurred in the 56b stand, at the Sky Oaks Biological Field Station (Fig. 4). The lowest shoot production occurred in the 32 year old stand at Warner Springs for *C. greggii* and in the 87 year old stand at Sky Oaks in *A. fasciculatum*. Shoot biomass production of *A. fasciculatum* was also low in



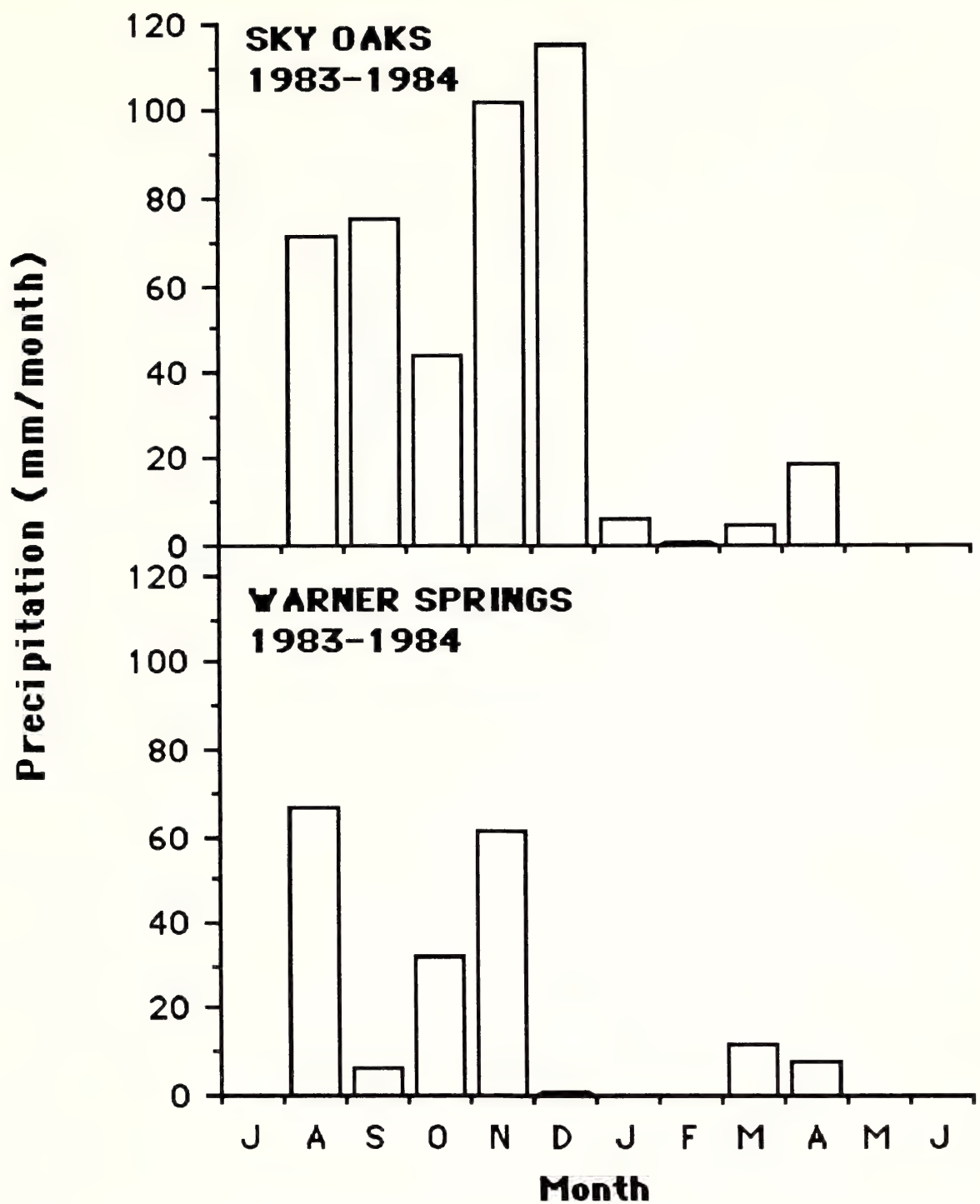


FIG. 1. Monthly precipitation (mm) for 1983-1984 at Warner Springs and Sky Oaks.

the 32 year old stand. Linear regressions of shoot production versus stand age did not indicate a significant change in production with increasing stand age in either one of the species ( $p > 0.25$  for both species).

DISCUSSION

Shoot production and shoot growth rates of *A. fasciculatum* and *C. greggii* were low compared to values reported earlier (Mooney et



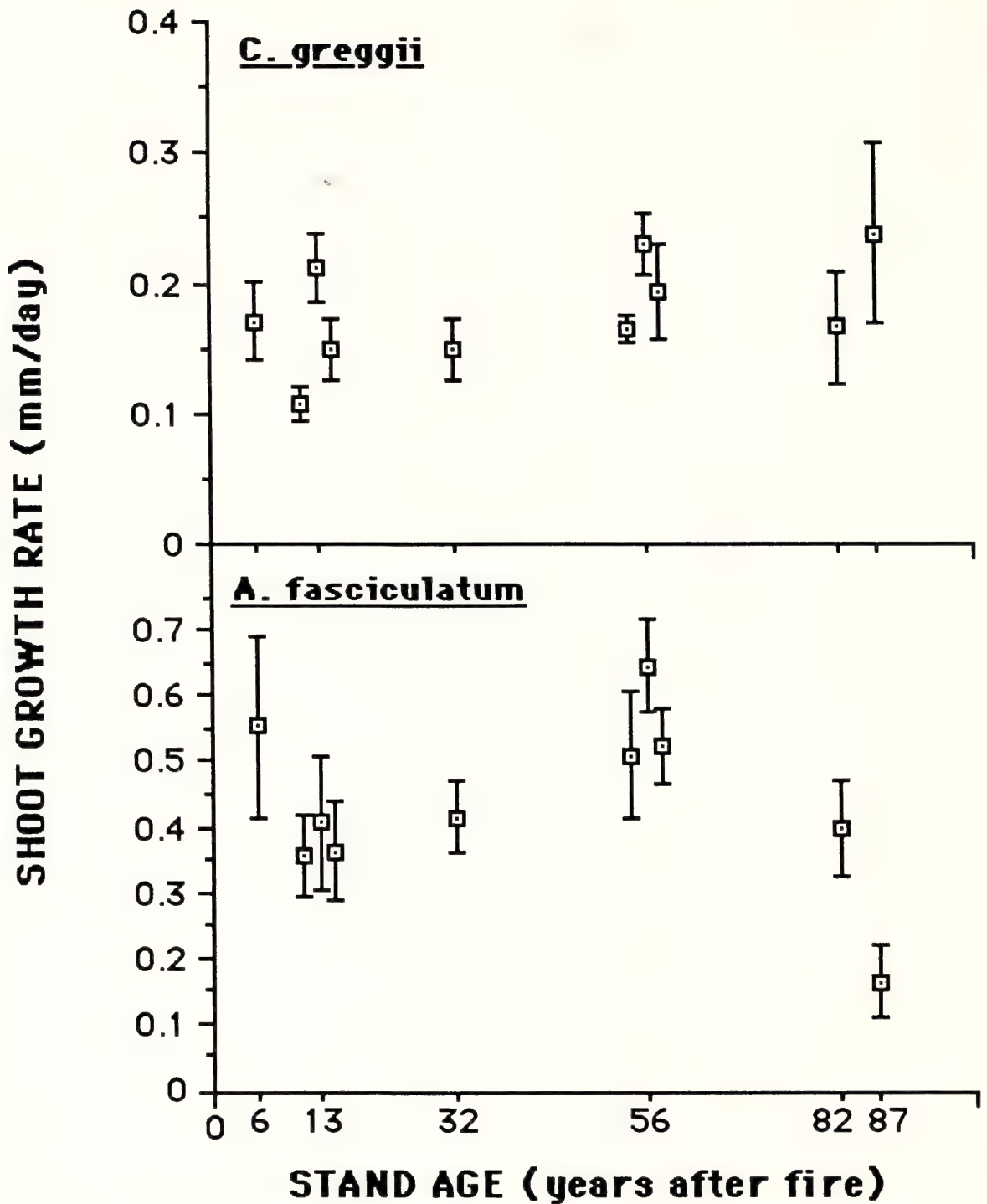


FIG. 2. Mean growth rates (mm/day) of 1984 shoots of *Ceanothus greggii* and *Adenostoma fasciculatum* in 10 chaparral stands differing in the number of years since they last burnt. There are 3 stands aged 13 years and 3 stands aged 56 years. Vertical lines indicate  $\pm$  one SE ( $n = 12$  shrubs per stand, except for *C. greggii* in stands 82 and 87 which had 4 and 6 shrubs, respectively, and *A. fasciculatum* in the 56b stand which had  $n = 11$ ).

al. 1977; McMaster et al. 1982; Table 2). Shoot growth rates of two evergreen sclerophylls of the Chilean matorral, *Cryptocarya alba* and *Quillaja saponaria*, ranged from 1.3 mm/day to 0.6 mm/day respectively, with a seasonal rainfall of 650 mm/yr (Montenegro et al. 1979). Total shoot elongation over the growing season in *A.*



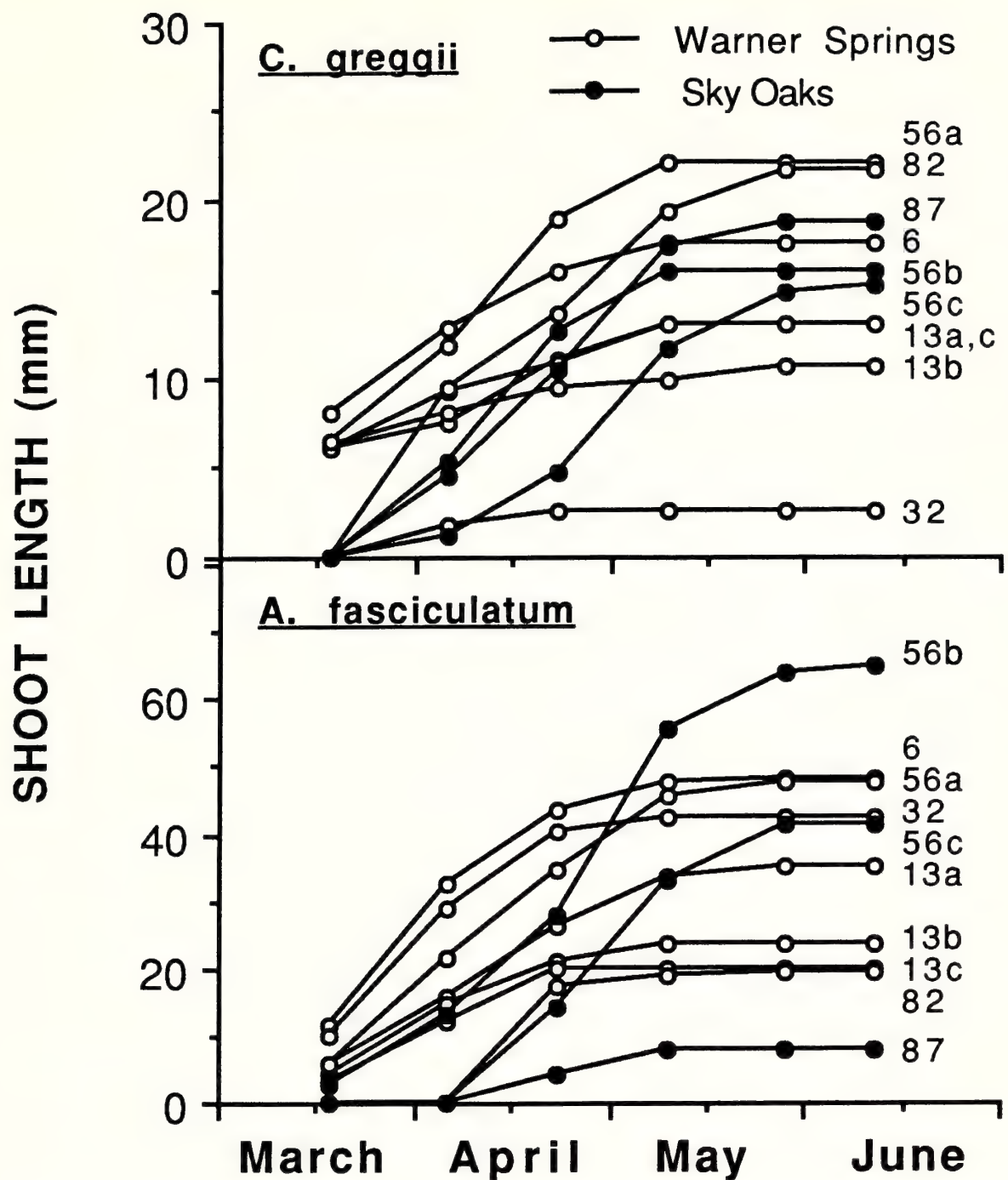


FIG. 3. Mean shoot length of *Ceanothus greggii* and *Adenostoma fasciculatum* throughout the 1984 growing season in the Sky Oaks (black dots) and the Warner Springs (white dots) stands. Stand ages are indicated at the end of each curve. The letters a, b, c for the stand ages 13 and 56 years correspond to the replicates of these stands. n = 12 shrubs per stand, except for *C. greggii* in stands 82 and 87 which had 4 and 6 shrubs, respectively, and *A. fasciculatum* in the 56b stand which had n = 11; shoot length of each shrub was based on 10 branches.

*fasciculatum* (10 to 60 mm) was much smaller than the value measured by Baker et al. (1982; 160 to 220 mm) in 1978, a rainy year. Rainfall during the 1983–1984 season at Warner Springs and Sky Oaks was much lower than in the previous year (711 and 1738 mm, respectively), and far below the precipitation level in the Echo Valley in 1973/74 (Mooney et al. 1977; Table 2) and in 1978/79 (McMaster



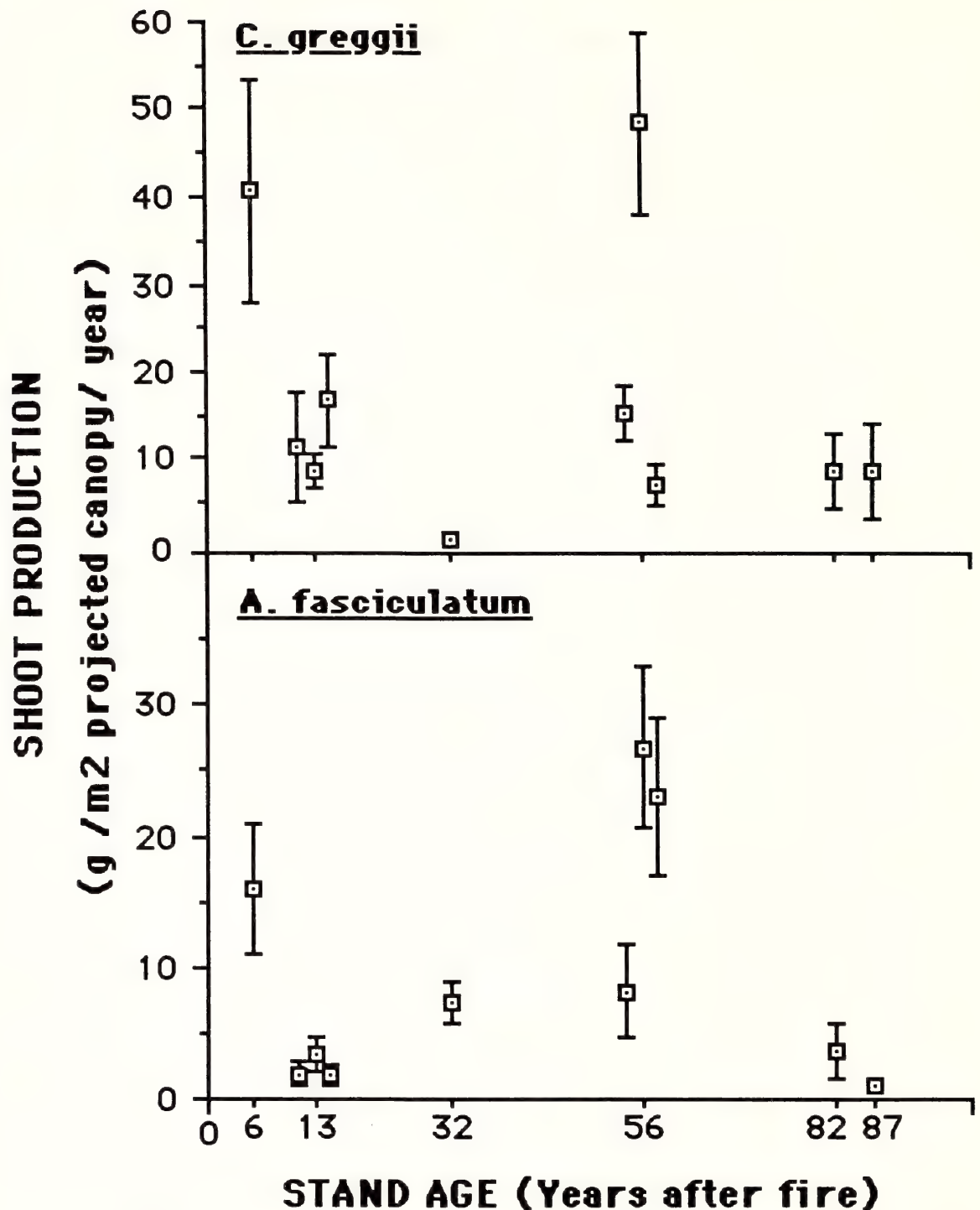


FIG. 4. Mean 1984 shoot biomass production (g dry weight/m<sup>2</sup> projected canopy area) of *Ceanothus greggii* and *Adenostoma fasciculatum* in 10 stands differing in the number of years since they last burnt. There are 3 stands aged 13 years and 3 stands aged 56 years. Vertical lines indicate  $\pm$  one SE ( $n = 12$  shrubs per stand, except for *C. greggii* in stands 82 and 87 which had 4 and 6 shrubs, respectively, and *A. fasciculatum* in the 56b stand which had  $n = 11$ ).

et al. 1982). The low growth rates observed in this study may be a consequence of the low rainfall in the winter of 1983–1984. The drought year 1972/73 in southern California caused significant reductions of leaf initiation, i.e., new shoot development, in *C. greggii* and *A. fasciculatum* (Hoffmann et al. 1977). Mooney et al. (1977)



TABLE 2. MEAN SHOOT PRODUCTION, SHOOT GROWTH RATE (mm/day) IN *ADENOSTOMA FASCICULATUM* (AF), AND *CEANOTHUS GREGGII* (CG) IN SOUTHERN CALIFORNIA CHAPARRAL AT ECHO VALLEY (Mooney et al. 1977; McMaster et al. 1982) and at Sky Oaks and Warner Springs (this study). Precipitation was measured between October and April. Ranges of values obtained for the three 13-year-old and the three 56-year-old stands are indicated.

| Year of study | Stand age (years) | Shoot production g/m <sup>2</sup> projected area/yr |      | Shoot growth rate (mm/day) |         | Precipit. (mm) | Source                 |
|---------------|-------------------|---|------|----------------------------|---------|----------------|------------------------|
|               |                   | Cg  | Af   | Cg                         | Af      |                |                        |
| 1973          | 20                | 860   | 541  |                            |         | 650            | Mooney et al. (1977)   |
| 1978          | 25                | 700   | 280  |                            |         | 843            | McMaster et al. (1982) |
| 1979          | 26                |   | 350  | 5.4                        | 1.0     | 722            | McMaster et al. (1982) |
| 1984          | 13                | 8-17  | 2-3  | 0.1-0.2                    | 0.3-0.4 | 113            | This study             |
| 1984          | 56                | 7-48  | 8-27 | 0.2                        | 0.5-0.6 | 113-292        | This study             |



report that in the drought year of 1972, production in California chaparral was only about 15 percent of that during the rainy year of 1973.

None of the measurements performed in this study showed any correlation with stand age. Data collected on chaparral shrubs by Keeley and Keeley (1977) and Zammit and Zedler (pers. comm.) did not show a decline of shrub vigor with age either. Measurements of shoot biomass production similar to ours on an obligate seeder, *Arctostaphylos glauca*, and a resprouter *Arctostaphylos glandulosa*, gave similar values in a 23 year old stand and a 90 year old stand (Keeley and Keeley 1977). *Arctostaphylos glauca* produced slightly less vegetative biomass but more reproductive biomass in the 90 year old stand compared to the 23 year old stand. Zammit and Zedler showed that there is no decline in seed production in *C. greggii* from 6 to 82 years after fire. It is possible that the lack of differences in growth rates with age in our study was due to the very limiting water availability. Seasonal shoot elongation lasts longer in young than in old trees (Kramer and Kozlowski 1979). Seasonal duration of shoot elongation in this study was not related to stand age but seemed to be more dependent on physical stand characteristics; shrubs in the Sky Oaks stands generally reached maximum shoot length later in the season, probably because the sites in Sky Oaks were in average 300 m higher than the sites in Warner Springs.

Variability in new shoot biomass production appeared as high among stands of the same age as among stands of different ages. For example, shoot production in *C. greggii* in the 56-yr-old stands varied between 7 and 48.5 g/m<sup>2</sup> projected canopy area and shoot production between stands varied between 1 and 48.5 g/m<sup>2</sup> projected canopy area. This suggests that stand characteristics other than age played a major role in shoot biomass production, and illustrates the difficulties that arise in the use of fire-induced age sequences (see Zedler and Zammit 1989). The high production of *C. greggii* in the 56b stand may have been due to two factors which differed from the other nine stands. 1) Ash may have been deposited from a fire that occurred in an adjacent stand in January, 1984 prior to the 1984 growing season and 2) the 56b stand was on the Tollhouse rather than the Sheephead soil series. Analyses of soil moisture retention at the Sky Oaks Biological Field Station (Greenwood 1983) indicated that soils of the Tollhouse series have a greater soil moisture retention than those of the Sheephead series, which could greatly benefit plant growth in a very dry year.

We had asked initially if shoot growth rates and shoot production of *C. greggii* and *A. fasciculatum* would decline with increasing stand age. No sign of decreased shrub vigor could be detected in either one of the shrub species. These data suggest that *C. greggii* is not a short lived species. If, as it is commonly assumed, *C. greggii* are



eliminated from older stands, it might be for reasons other than the physiological decline of the shrub. For example, as nutrient availability declines with time after fire (Marion and Black 1988), *C. greggii* might be outcompeted because of its shallow root system. Repetition of this experiment in a year with average or greater rainfall might however reveal differences in shrub vigor that were suppressed by the lack of soil moisture.

#### LITERATURE CITED

- BAKER, G. A., P. W. RUNDEL, and D. J. PARSONS. 1982. Comparative phenology and growth in three chaparral shrubs. *Bot. Gaz. (Crawfordsville)* 143:94–100.
- GREENWOOD, N. 1983. Soils of the Sky Oaks Ranch. Pp. 50–62 in W. C. Oechel (ed.), *Sky Oaks biological station baseline studies*. San Diego State University, San Diego, California.
- HANES, T. L. 1971. Succession after fire in the chaparral of southern California. *Ecol. Monogr.* 41:27–52.
- HILBERT, D. W. and A. LARIGAUDERIE. 1990. The concept of stand senescence in chaparral and other mediterranean type ecosystems. *Oecologia plantarum* 11: 181–190.
- HOFFMAN, A., H. A. MOONEY, and J. KUMMEROW. 1977. Qualitative phenology. Pp. 102–120 in N. J. W. Thrower and D. E. Bradbury (eds.), *Chile-California mediterranean scrub atlas*. US/IBP Synthesis Series No. 2. Dowden, Hutchinson, and Ross, Inc., Stroudsburg, Pennsylvania.
- JOW, W. M., S. S. BULLOCK, and J. KUMMEROW. 1980. Leaf turnover rates of *Adenostoma fasciculatum* (Rosaceae). *Amer. J. Bot.* 67:256–261.
- KEELEY, J. E. 1975. Longevity of nonsprouting *Ceanothus*. *Amer. Midl. Naturalist* 93:504–507.
- and S. C. KEELEY. 1977. Energy allocation patterns of a sprouting and a nonsprouting species of *Arctostaphylos* in the California chaparral. *Amer. Midl. Naturalist* 98:1–10.
- KRAMER, P. J. and T. T. KOZLOWSKI. 1979. *Physiology of woody plants*. Academic Press, New York.
- MARION, G. M. and C. H. BLACK. 1988. Potentially available nitrogen and phosphorus along a chaparral fire cycle chronosequence. *Soil Sci. Soc. Amer. J.* 52: 1155–1162.
- MCMASTER, G. S., W. M. JOW, and J. KUMMEROW. 1982. Response of *Adenostoma fasciculatum* and *Ceanothus greggii* chaparral to nutrient additions. *J. Ecol.* 70: 746–756.
- MONTENEGRO, G., M. E. ALJARO, and J. KUMMEROW. 1979. Growth dynamics of chilean matorral shrubs. *Bot. Gaz. (Crawfordsville)* 140:114–119.
- MONTYGIERD-LOYBA, T. M. and J. E. KEELEY. 1987. Demographic structure of *Ceanothus megacarpus* chaparral in the long absence of fire. *Ecology* 68:211–213.
- MOONEY, H. A. and J. KUMMEROW. 1977. Quantitative phenology. Pp. 121–125 in N. J. W. Thrower and D. E. Bradbury (eds.), *Chile-California mediterranean scrub atlas*. US/IBP Synthesis Series No. 2. Dowden, Hutchinson, and Ross, Inc., Stroudsburg, Pennsylvania.
- , ———, A. W. JOHNSON, D. J. PARSONS, S. KEELEY, A. HOFFMAN, R. I. HAYS, J. GILBERTO, and C. CHU. 1977. The producers—their resources and adaptive responses. Pp. 85–143 in H. A. Mooney (ed.), *Convergent evolution in Chile and California: Mediterranean climate ecosystems*. US/IBP Synthesis Series No. 5. Dowden, Hutchinson, and Ross, Inc., Stoudsburg, Pennsylvania.
- NOODÉN, L. D. 1988. Whole plant senescence. Pp. 392–439 in L. D. Noodén and A. C. Leopold (eds.), *Senescence and aging in plants*. Academic Press, San Diego.



- PARSONS, D. J. 1976. The role of fire in natural communities: an example from the southern Sierra Nevada, California. *Environm. Conserv.* 3:91–99.
- RUNDEL, P. W. and D. J. PARSONS. 1979. Structural changes in chamise (*Adenostoma fasciculatum*) along a fire-induced age gradient. *J. Range Managem.* 32:462–466.
- and ———. 1980. Nutrient changes in two chaparral shrubs along a fire-induced age gradient. *Amer. J. Bot.* 67:51–58.
- ZEDLER, P. and C. A. ZAMMIT. 1989. A population-based critique of concepts of change in the chaparral. Pp. 73–84 in S. C. Keeley (ed.), *The California chaparral, paradigms reexamined*. Natural History Museum of Los Angeles County, Los Angeles, California.
- (Received 18 Dec 1989; revision accepted 6 Aug 1990.)

---

## NORTHWORTHY COLLECTIONS

### MEXICO: BAJA CALIFORNIA SUR

*CALOGLOSSA LEPRIEURII* (Montagne). J. Agardh (Rhodophyta, Ceramiales, Delesseriaceae) Bahia Balandra (24°18'N, 110°15'W) near La Paz, 6 Jan 1990, *West 3033* (UC) and San Carlos, Bahia Magdalena (24°48'N, 112°07'W) 7 Jan 1990, *West 3025* (UC) abundant and conspicuous with *Bostrychia radicans* (Montagne) Montagne growing on *Rhizophora mangle* L. prop roots. Plants in both collections were tetrasporophytes. No gametophytes were seen.

*Significance.* *Caloglossa leprieurii* is distributed very widely in tropical and warm temperate oceans principally in association with mangroves. In his extensive field observations and collections in Baja California E. Y. Dawson seemingly had little interest in the mangroves that are distributed along the peninsula because he never reported *Caloglossa* (Allan Hancock Pacific Expeditions 26(1):207 pp, 1962). Furthermore his records of *Bostrychia radicans* are based on collections by Drouet and Richards in Sonora and his own collections in Jalisco and Nayarit along the mainland coast of Mexico. He did not record it from Baja California. Other more recent investigators (Huerta-Muzquiz and Mendoza-Gonzalez. *Phytologia* 59:35–57, 1985) working in the La Paz area also have overlooked *C. leprieurii* although they observed *B. radicans* which generally is much more abundant.—JOHN A. WEST and GIUSEPPE ZUCCARELLO, Department of Plant Biology, University of California, Berkeley, CA 94720.



DEMOGRAPHIC STRUCTURE OF  
CALIFORNIA BLACK WALNUT  
(*JUGLANS CALIFORNICA*; JUGLANDACEAE)  
WOODLANDS IN SOUTHERN CALIFORNIA

JON E. KEELEY

Department of Biology, Occidental College,  
Los Angeles, CA 90041

ABSTRACT

Three woodlands dominated by California black walnut were studied. At one site, *Quercus agrifolia* was a co-dominant whereas at the other two sites *Juglans californica* dominated >90% of the relative areal coverage. *Heteromeles arbutifolia* was a significant component of all three woodlands. At two of the sites most of the walnuts were single-stemmed and some of them exceeded 15 m in height. Another site was a more open savanna type woodland and many trees had multiple stems; 40% had 4 or more stems per plant and one had 16 stems. The age structure of the three *Juglans* populations is presented. At all sites there were stems at least 70 years of age. All populations had substantial seedling recruitment and densities ranged from 275 to 1975 seedlings (defined as stems  $\leq 5$  years of age and not attached to a mature tree) per hectare. It is hypothesized that irregularities in annual seedling establishment and seedling mortality play an important role in structuring these populations.

California black walnut (*Juglans californica*, nomenclature according to Munz 1974) is a low growing hardwood tree endemic to southern California. Woodlands dominated by this walnut occur in the southern Santa Inez and Santa Susana Mountains of Ventura Co. and the eastern-most portion of the Santa Monica Mountains and foothills of eastern Los Angeles Co. Most of these woodlands occur below 500 m although well-developed walnut woodlands may extend up to 1000 m (e.g., the north side of Oat Mt. in the Santa Susana Mts.). Outside of this range, *J. californica* occurs more often as scattered individuals amongst other hardwoods which form the Southern Oak Woodland Community. *Juglans californica* extends eastward to the western flanks of the San Bernardino Mts. and south to northern San Diego Co. (Beauchamp 1986). The northern limit of distribution appears to be central Santa Barbara Co.; reports of the species in San Luis Obispo Co. are considered to be either ascribable to *J. hindsii* (Jeps.) Jeps. (Hoover 1970) or plantings (Griffin and Critchfield 1972). The tree has been used in southern California as a rootstock for commercial walnut crops, and it has been widely planted in urban forestry projects, e.g., in the western Santa Monica Mountains (Radtke 1978).

Despite widespread current interest in California hardwoods, *Ju-*



*Juglans californica* woodlands have not received much attention. Apart from a few papers on the systematic affinities (Jepson 1908, 1917; Thomsen 1963) the only studies are two unpublished master's theses (Swanson 1967; Leskinen 1972). Throughout its range this species tends to be best developed on N-facing slopes with deep, well developed soils with high water-holding capacity derived from Tertiary marine shales. On many sites it is closely associated with two other tree species, *Quercus agrifolia* and *Heteromeles arbutifolia* (the latter is often associated with adjacent chaparral communities where, due to frequent fires, it is a shrub). Swanson (1967) reported that *Juglans* seedling reproduction was absent in the Los Angeles Co. population he studied and suggested this was due to low precipitation.

Due to urban sprawl much of the California black walnut woodland has been destroyed or is threatened, and it is considered to be one of California's rare and imperiled natural communities (Jones & Stokes Associates 1987). An understanding of the age structure of such woodlands is an important first step towards evaluating the reproductive status and, thus, the future health of the remaining remnant woodland stands. The focus of this study was to assess the age structure of three *Juglans californica* stands.

#### STUDY SITES AND METHODS

*Study sites.* Three sites of one to several hectares of walnut woodland were located as follows. 1, N-facing slope of Sulphur Mt. (350 m elev.) W of Hwy 150, 10 km N of Santa Paula, Ventura Co.; 2, N-facing slope of Mt. Washington (250 m), 3 km NE of Elysian Park, city of Los Angeles, Los Angeles Co.; 3, E-facing slope (225 m) in Montecito Park, 5 km SW of South Pasadena, city of Los Angeles, Los Angeles Co.

*Methods.* At each site, 18 10 × 10 m plots were randomly located and the basal diameter of stems of all tree and large shrub species within the plots was recorded. Stems connected to the same root-crown were indicated and the height and diameter of the canopy of each individual was recorded. Heights of trees beyond the reach of a 4 m pole were determined by calculation from the geometric relationship between angle to the top of the tree (measured with an inclinometer) and distance to the tree along the same contour. At each site nine to 10 *Juglans* trees were cored at 25 cm above the ground with an increment borer and the basal diameter, areal diameter and height were recorded. Also, 18 seedlings and saplings, too small to be cored, were cut and a section of the stem near the base was removed. The increment cores and stem sections were returned to the lab for ring counts.

The quadrat data were analyzed for community indices of density and coverage for all woody species. Basal coverage and areal cov-



TABLE 1. RELATIVE AREAL COVERAGE, BASAL AREA COVERAGE, AND DENSITY FOR *JUGLANS CALIFORNICA* DOMINATED WOODLAND ON THE NORTH-FACING SLOPE OF SULPHUR MT., VENTURA COUNTY, CALIFORNIA.

| Species                        | Relative areal coverage (%) | Basal area coverage (m <sup>2</sup> /ha) | Density (no./ha) |             |
|--------------------------------|-----------------------------|--|------------------|-------------|
|                                |                             |  | Stems            | Individuals |
| <i>Juglans californica</i>     |                             |  |                  |             |
| Alive                          | 49                          | 11.4                                     | 3925             | 3500        |
| Dead                           | <1                          | <0.1                                     | 50               | 50          |
| <i>Quercus agrifolia</i>       | 39                          | 38.2                                     | 1390             | 1240        |
| <i>Heteromeles arbutifolia</i> | 12                          | 1.6                                      | 1450             | 1140        |
| <i>Sambucus mexicana</i>       | <1                          | <0.1                                     | 90               | 80          |
| <i>Rhamnus crocea</i>          | <1                          | <0.1                                     | 30               | 30          |

erage were calculated by assuming the trunks and canopies approximated a circle. Densities of stems (ramets) as well as individuals (genets) were calculated. The *Juglans* cores and stem sections were sanded and the number of rings determined. On older stems the coloration of the heartwood made ring counts impossible without first bleaching with a 5% solution of sodium hypochlorite. It was assumed that rings were laid down annually, a reasonable assumption for a temperate climate deciduous tree, and true for other trees in southern California (Schulman 1947). A regression analysis of age and basal diameter was done using a linear regression and polynomial regression program available on BMDP (Brown 1977). The equation giving the best fit was used to predict the ages of all *Juglans* stems recorded in the quadrats.

RESULTS

There were marked differences in the community characteristics of the three walnut woodlands. At the Sulphur Mt. Site (Table 1) *Quercus agrifolia* (coast live oak) was a co-dominant whereas at the other two sites (Tables 2 and 3) *Juglans californica* was the only dominant. At Sulphur Mt. areal coverage was estimated to be greater for walnut but due to the massive trunks of several of the live oaks, basal area coverage was substantially greater for that species. At this site the *J. californica* were nearly all single stemmed and thus the number of individual genets was similar to the number of stems (ramets) (Table 1). Although *Juglans* was the only dominant at the other two sites (Tables 2 and 3) there were marked differences between these two stands. At the Mt. Washington Site *J. californica* basal area coverage was double that recorded at Montecito Park whereas the latter site had more than double the number of stems as the Mt. Washington Site. In other words the Mt. Washington Site



TABLE 2. RELATIVE AREAL COVERAGE, BASAL AREA COVERAGE, AND DENSITY FOR *JUGLANS CALIFORNICA* DOMINATED WOODLAND ON THE NORTH-FACING SLOPE OF MT. WASHINGTON, LOS ANGELES COUNTY, CALIFORNIA.

| Species                        | Relative areal coverage (%) | Basal area coverage (m <sup>2</sup> /ha) | Density (no./ha) |             |
|--------------------------------|-----------------------------|--|------------------|-------------|
|                                |                             |  | Stems            | Individuals |
| <i>Juglans californica</i>     |                             |  |                  |             |
| Alive                          | 90                          | 38.4                                     | 1360             | 1130        |
| Dead                           | <1                          | 0.1                                      | 50               | 50          |
| <i>Heteromeles arbutifolia</i> | 8                           | 3.4                                      | 410              | 150         |
| <i>Prunus ilicifolia</i>       | 2                           | 0.6                                      | 220              | 200         |

was a woodland of large, mostly single-stemmed, trees whereas the Montecito Park Site was a more open woodland with many smaller, multiple-stemmed trees and a greater number of dead *Juglans* trunks. At all sites *Heteromeles arbutifolia* was a significant component of these woodlands. *Sambucus mexicana*, *Rhamnus ilicifolia*, *Prunus ilicifolia*, and *Toxicodendron diversilobum* were present at all three sites, although they were not always recorded from the plots. Swanson (1967) reported putative hybrids between *J. californica* × *J. regia* from an area on Sulphur Mt.; however, I did not observe any at the Sulphur Mt. Site.

The distribution of stem diameters of the three co-dominants at Sulphur Mt. showed marked differences. For *J. californica* (Fig. 1) there was more continuous distribution of size classes (up to 85 mm) compared to that for *Q. agrifolia* (Fig. 1). This coast live oak population had 90% of the stems in the smallest size class and very few greater than 25 mm. The maximum stem diameter was 1000 mm for *Q. agrifolia* which was nearly three times greater than the largest *J. californica* and six times greater than the largest *H. arbutifolia* (Fig. 1).

The tallest *J. californica* trees were 11 m although only 10% of the population was greater than 5 m. *Quercus agrifolia* reached 18 m and 10% were taller than 10 m. Several of the *Heteromeles arbutifolia* were 10 m in height.

At the Sulphur Mt. Site, 27 *Juglans* stems were aged and the oldest was 98 years. Age was significantly correlated with all of the parameters measured: basal diameter (Fig. 2), areal diameter (Fig. 2) and height (Fig. 2). The relationship between age and areal canopy diameter was best described by a linear equation whereas the relationship between age and basal diameter or age and height best fit a higher order polynomial equation. The regression equation relating age and basal diameter was used to estimate the ages of the



TABLE 3. RELATIVE AREAL COVERAGE, BASAL AREA COVERAGE, AND DENSITY FOR *JUGLANS CALIFORNICA* DOMINATED WOODLAND ON AN EAST-FACING SLOPE IN MONTECITO HEIGHTS, LOS ANGELES COUNTY, CALIFORNIA.

| Species                        | Relative<br>areal<br>coverage<br>(%) | Basal area<br>coverage<br>(m <sup>2</sup> /ha) | Density (no./ha) |             |
|--------------------------------|--------------------------------------|--|------------------|-------------|
|                                |                                      |  | Stems            | Individuals |
| <i>Juglans californica</i>     |                                      |  |                  |             |
| Alive                          | 95                                   | 19.6   | 2790             | 1710        |
| Dead                           | 3                                    | 4.2  | 478              | 100         |
| <i>Heteromeles arbutifolia</i> | 1                                    | 0.1  | 78               | 20          |
| <i>Prunus ilicifolia</i>       | 1                                    | <0.1   | 20               | 10          |

*Juglans* stems recorded from the quadrats and these are shown in Fig. 3. The oldest trees encountered in the sampling were estimated to be about 73 years of age. Fifty percent of the population, or 1975/ha, were estimated to be seedlings (defined as stems  $\leq 5$  years of age and not attached to a matured tree). This seedling pool had an areal canopy diameter of  $\leq 0.5$  m and 20% of this cohort exceeded 1.0 m in height. There were gaps in some age classes but most were represented and the decrease in density with age best fit a negative third order polynomial relationship ( $p < 0.001$ ,  $r = 0.95$ ).

At the Mt. Washington Site stem diameters of *Juglans* were significantly larger than those observed at Sulphur Mt. with the largest being 900 mm. Heights of these trees were also greater; one tree was 15.5 m and 10% of the population exceeded 8 m. The same pattern of larger trees at this site was observed for *H. arbutifolia*. One stem had a basal diameter of 575 mm and a height of 11 m. The only other woody species recorded was *Prunus ilicifolia* although many of the specimens appeared to be hybrids with *P. lyonii* (a Channel Island endemic) which grew at the site and may have escaped from cultivation or been planted by aerial spraying (Radtke 1978). At this site the largest *Juglans* stem cored was rotted in the middle so the exact age was unknown. From the intact cores, a linear model was the best fit between age and basal diameter. Using this equation the largest *Juglans* stem encountered in the quadrat sampling was estimated to be 132 years of age (Fig. 3). Only 25% of the stems (275/ha) were 1–5 year old seedlings and the decrease in density of older age classes approximated a second order polynomial curve ( $p < 0.01$ ,  $r = 0.94$ ).

At the Montecito Park Site the largest *Juglans* stem had a diameter of 675 mm and was 10 m tall. The largest *Heteromeles* stem had a basal diameter of only 71 mm. The oldest *Juglans* stem aged was 81 years of age and a linear model was the best fit for the age/



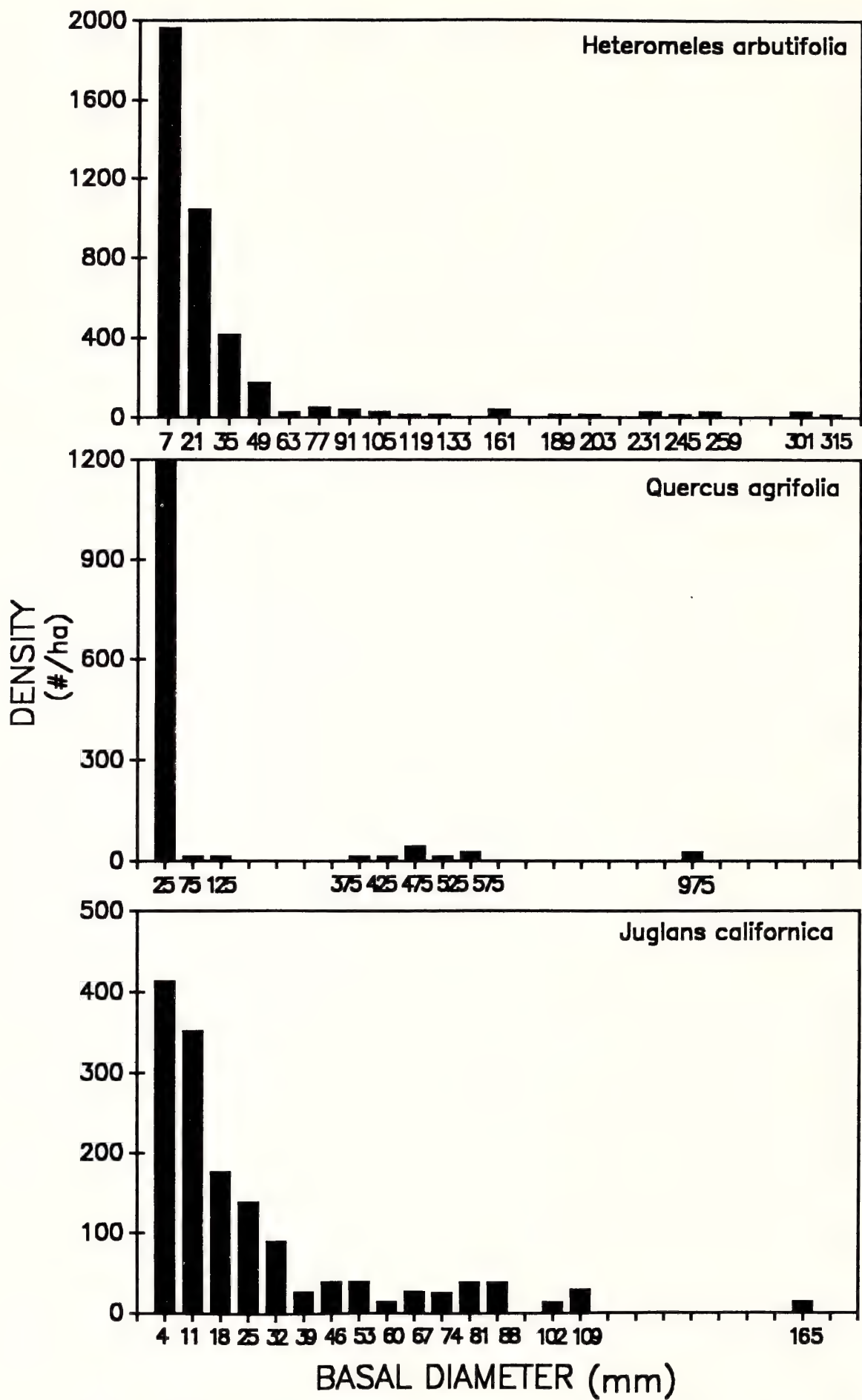


FIG. 1. Frequency distribution of stem diameters for *Juglans californica*, *Quercus agrifolia*, and *Heteromeles arbutifolia* at the Sulphur Mt. Site.



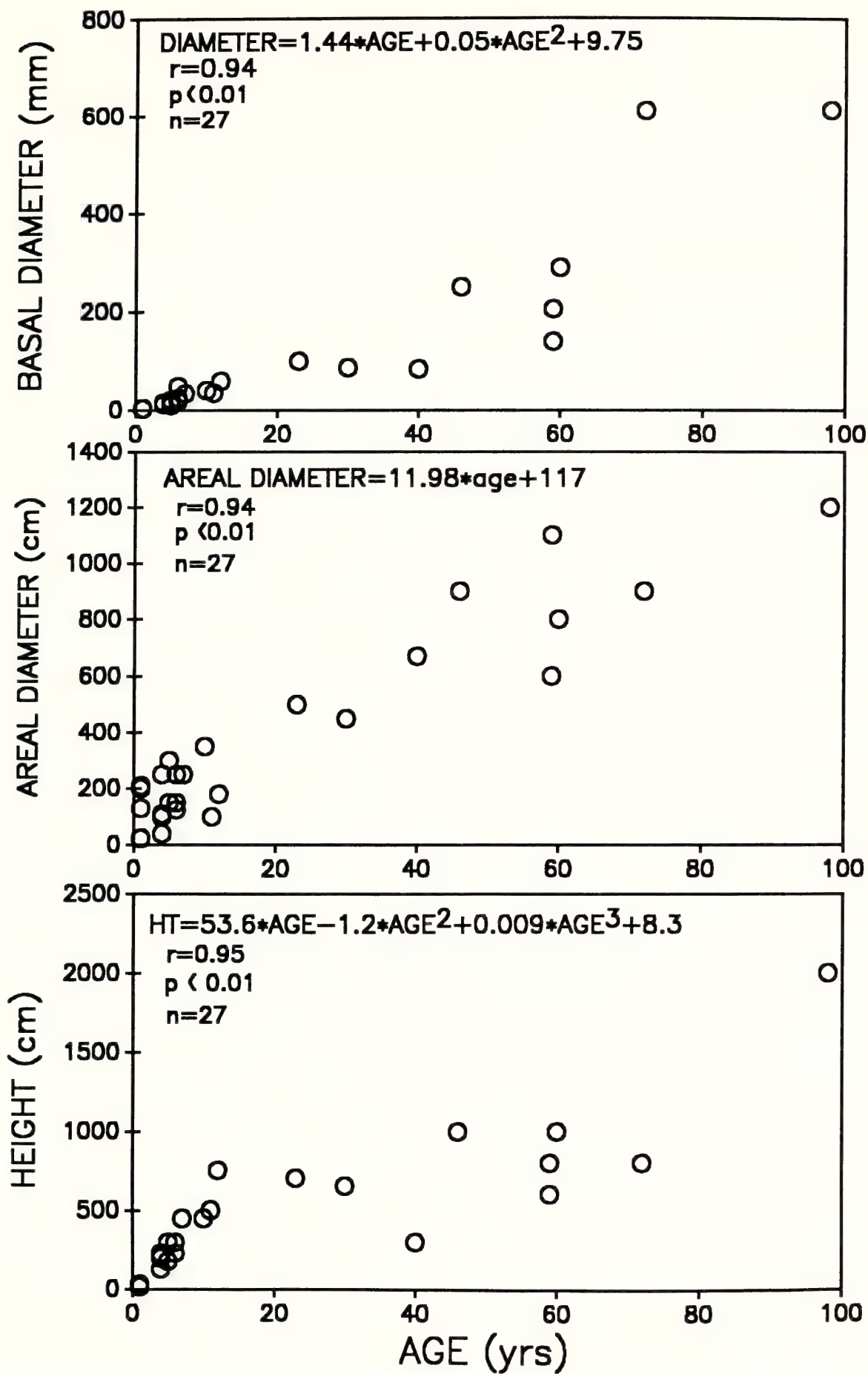


FIG. 2. Relationship between age and height, areal diameter, and basal diameter, for *Juglans californica* at the Sulphur Mt. Site.



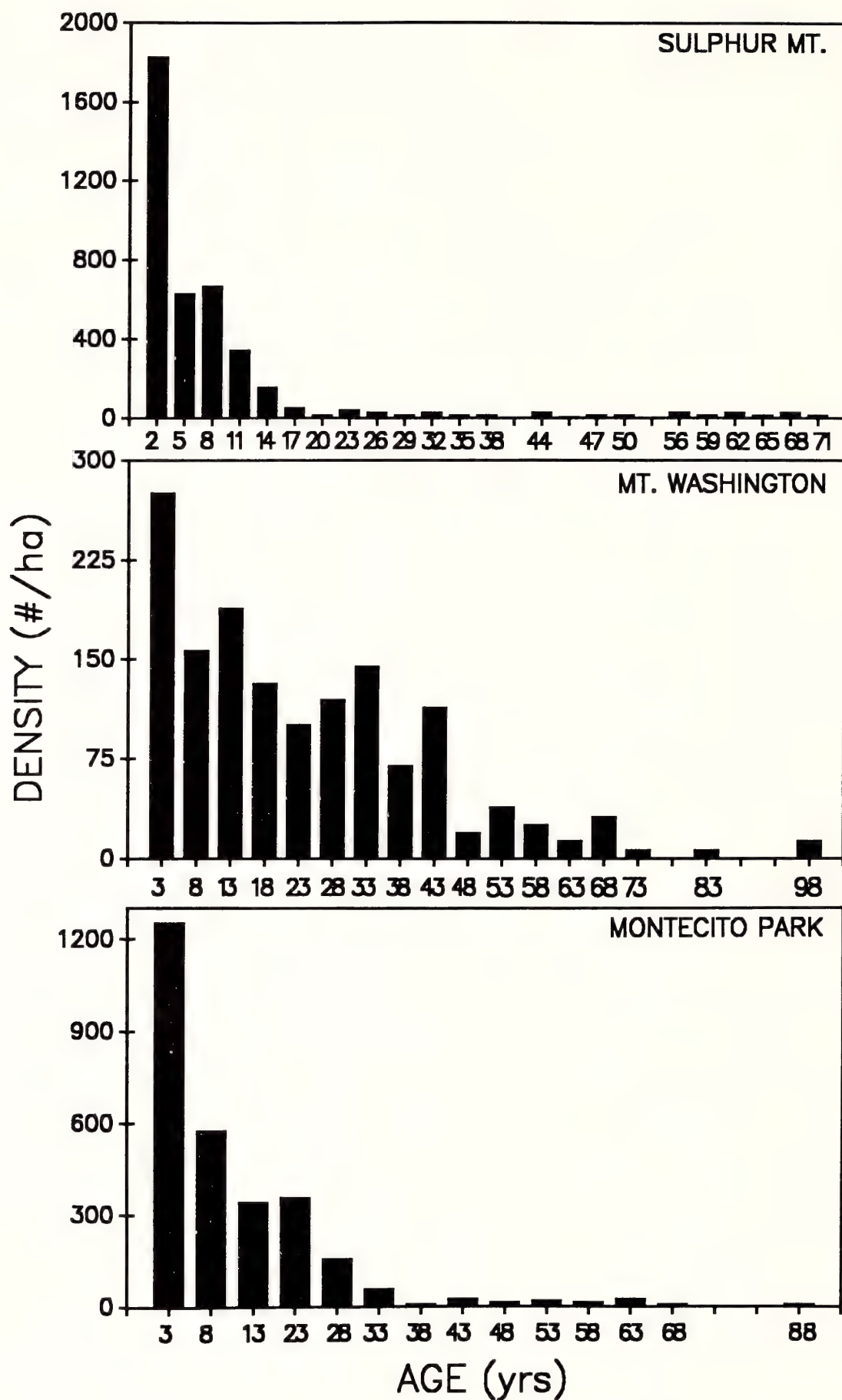


FIG. 3. Estimated age structure of *Juglans californica* stems at the three study sites (live = solid bar, dead = open bar). Age of stems recorded in the random quadrat sampling was predicted from the equations: Sulphur Mt. Site: Age =  $0.313 \cdot \text{Diameter}$



diameter relationship. This equation predicted the oldest tree sampled in the quadrats was 77 years (Fig. 3) and that 45% of the population of *Juglans* stems (1250/ha) were  $\leq 5$  years of age. There was a very rapid drop in density of older age classes which approximated a third order polynomial curve ( $p < 0.001$ ,  $r = 0.97$ ). As can be seen in Table 3, there were many more stems than individual genets at this site. Seedlings and saplings were seldom multiple-stemmed, rather these were generally the larger trees. Of these, 40% had four or more stems and one tree had 16 stems. The age-structure of individual genets, as reflected in a histogram of the oldest stem on each genet (not shown), was compared with the histogram for all stems (Fig. 3). The shape of these histograms was remarkably similar and the number of individual genets  $\leq 5$  years (i.e., seedlings) was 51% of the population or 860/ha.

### DISCUSSION

Black walnut woodlands in southern California may be dominated by *Juglans californica* alone or walnuts associated with sclerophyllous evergreen trees. The most common ones reported in this study, *Quercus agrifolia* and *Heteromeles arbutifolia*, have also been reported from other studies (Swanson 1967; Leskinen 1972; Campbell 1980). Axelrod (1977) contends that this *Juglans* dominated woodland is quite ancient, dating back to at least the Miocene when it was associated with an even greater array of evergreen broadleaf trees.

A number of the evergreen trees and shrubs currently associated with *Juglans* woodlands, e.g., *Heteromeles arbutifolia*, *Prunus ilicifolia*, and *Rhamnus ilicifolia*, are common elements in the widespread chaparral community which is often juxtaposed with walnut woodlands. These evergreens persist in the fire-prone chaparral due to their proclivity to resprout after fire. The reproductive biology of these evergreens, however, is poorly adapted to this community in that the seeds have no imposed dormancy and thus germinate readily after dispersal. These seedlings do not survive in most chaparral stands; consequently, seedling reproduction by these species is seldom observed in chaparral. Reports of reproduction are usually restricted to extremely old chaparral (Keeley and Keeley 1988) or woodlands, as observed in this study. These taxa persist in walnut woodlands, as well as other broadleaf woodlands (Campbell 1980), as "gap-phase" species, which is consistent with the fact that these

---

←

—  $0.00029 \cdot \text{Diameter}^2 + 0.08$  ( $p < 0.001$ ,  $r = 0.96$ ,  $n = 27$ ); Mt. Washington Site: Age =  $0.141 \cdot \text{Diameter} + 4.77$  ( $p < 0.001$ ,  $r = 0.91$ ,  $n = 25$ ); Montecito Park Site: Age =  $0.126 \cdot \text{Diameter} + 3.59$  ( $p < 0.001$ ,  $r = 0.93$ ,  $n = 23$ ).



species produce bright, red, bird-dispersed berries unlike most other chaparral taxa. These evergreen taxa have been part of oak woodlands and the mixed evergreen forest since at least Miocene (Axelrod 1977) and today are still considered to be "characteristic components" of four different woodland communities in California (Barbour and Major 1977).

The three sites studied here describe woodlands of quite different structure. The Montecito Park Site was the most open savanna-like woodland of the three sites. Total dominance of all woody species (as measured by basal area coverage) was less than half that observed at the other two sites. Records of prior disturbance in this area are non-existent. Observations of the surrounding hills, which are dominated by *Brassica nigra* and other non-native annuals with remnants of a few resprouting chaparral shrubs, suggests this area has burned frequently in the past; a characteristic of much of the Los Angeles Basin (Freudenberger et al. 1987). The savanna-like aspect of the Montecito Park Site may be due to such disturbance. The multiple-stem character of most of the walnut trees at that site would be consistent with that hypothesis since this species resprouts readily after burning. In addition, the significant number of sizeable dead *Juglans* at this site (Table 3) compared to very few at the older Mt. Washington Site (Table 2) also supports the idea that fires have been a part of the Montecito Site's history.

The Mt. Washington Site is an example of a more closed-canopy type woodland with a much greater dominance of *Juglans*. The structure of this woodland suggests it has been free from disturbance for an extended period of time. Most of the walnuts are single-stemmed and there are many large specimen trees, both *J. californica* and *H. arbutifolia*, of extraordinary size. There was no obvious evidence of fire at this site in recent decades as was true of the Sulphur Mt. Site, which likewise had mostly single-stemmed walnut trees.

Seedling regeneration of *Juglans* was evident at all three sites. The density of seedlings at Sulphur Mt. was similar to that observed by Swanson (1967) for a site near our Sulphur Mt. site. Neither of the Los Angeles Co. sites described here lacked seedling reproduction as Swanson (1967) reported for his Brea Canyon site in eastern Los Angeles Co. He hypothesized that this lack of *Juglans* seedling establishment was due to the lower precipitation in the southern part of its range. His hypothesis seems unlikely in light of the continuous seedling establishment apparent over the past several decades in the two Los Angeles Co. sites described here (Fig. 3). Intensive cattle grazing present at Swanson's (1967) Brea Canyon Site may account for lack of seedling recruitment there; grazing in recent decades has not been a factor at any of the sites described here. The large seedling population observed at the Montecito Park Site suggests that, if protected from fire, eventually this savanna-like woodland may develop into a denser woodland.



Interpretation of the age structures reported here requires careful analysis. If we assume that all three populations have constant rates of annual recruitment, and mortality is constant with age, we could conclude that these populations are relatively stable. That is, barring disturbance, recruitment and survival of seedlings and saplings is sufficient to maintain these populations in the future. If these assumptions were true one could account for gaps in certain age classes by a low intensity disturbance such as a ground fire which selectively eliminated seedlings during those years but failed to kill older age classes. Such a hypothesis seems unlikely since, due to the low canopies and lack of self-pruning in these walnuts, fires generally are much more intense and consume the entire canopy of the forest.

In general, a model of constant recruitment and constant mortality is probably a poor one for interpreting age structure of walnut populations. The shape of age-structures (Fig. 3) could be explained by an increase in fruit production as the trees in the forest age. This is an unlikely explanation since abundant fruit production is observed on trees after about 20 years (pers. obs.) plus the Mt. Washington stand with the largest and oldest trees did not have greater seedling production than the other two younger stands.

I suggest reproduction and mortality are not constants in these walnut populations and that they vary in a stochastic rather than a deterministic manner. Although no quantitative data exist on *Juglans californica* reproduction, one can readily observe years of little or no fruit production, commonly in drought years, in contrast to mast years of very heavy walnut production during wetter years. Since the seeds of this species have no imposed dormancy and germinate readily after dispersal (Keeley 1987), it follows that seedling establishment would not be constant from year to year. Due to the potentially lethal effect of occasional severe droughts, it seems likely that mortality is also not constant for all age cohorts. Thus, I hypothesize that gaps in certain age classes in some of the age structures presented here are due to annual variations in recruitment and mortality, resulting from annual differences in climate, especially precipitation.

#### ACKNOWLEDGMENTS

I thank Cheryl Swift for assistance in making figures, J. Griffin, V. L. Holland, and D. Keil for helpful comments on the ms and R. Quinn whose symposium talk stimulated completion of this project.

#### LITERATURE CITED

- AXELROD, D. I. 1977. Outline history of California vegetation. Pp. 139–194 in M. G. Barbour and J. Major (eds.), *Terrestrial vegetation of California*. John Wiley, New York.
- BARBOUR, M. G. and J. MAJOR (eds.). 1977. *Terrestrial vegetation of California*. John Wiley, New York. 1002 pp.



- BEAUCHAMP, R. M. 1986. A flora of San Diego County, California. Sweetwater River Press, National City, CA. 241 pp.
- BROWN, M. B. (ed.). 1977. BMDP-77. Biomedical computer programs. P-Series. Univ. Calif. Press, Los Angeles. 880 pp.
- CAMPBELL, B. 1980. Some mixed hardwood forest communities of the coastal ranges of southern California. *Phytocoenologia* 8:297–320.
- FREUDENBERGER, D. O., B. E. FISH, and J. E. KEELEY. 1987. Distribution and stability of grasslands in the Los Angeles basin. *Bull. So. Calif. Acad. Sci.* 86:13–26.
- GRIFFIN, J. R. and W. B. CRITCHFIELD. 1972. The distribution of forest trees in California. USDA Forest Service, Pac. Southw. For. Range Exp. Sta., Res. Pap. PSW-82. 114 pp.
- HOOVER, R. F. 1970. The vascular plants of San Luis Obispo County, California. Univ. Calif. Press, Los Angeles. 350 pp.
- JEPSON, W. L. 1908. The distribution of *Juglans californica* Wats. *Bull. S. Calif. Acad. Sci.* 7:23–24.
- . 1917. The native walnuts of California. *Madroño* 1:55–57.
- JONES & STOKES ASSOCIATES. 1987. Sliding toward extinction: the state of California's natural heritage. Jones & Associates, Sacramento, CA.
- KEELEY, J. E. 1987. Role of fire in seed germination of woody taxa in California chaparral. *Ecology* 68:434–443.
- and S. C. KEELEY. 1988. Chaparral. Pp. 165–207 in M. G. Barbour and W. D. Billings (eds.), *North American terrestrial vegetation*. Cambridge Univ. Press, Cambridge.
- LESKINEN, C. A. 1972. *Juglans californica*: local patterns in southern California. M.A. thesis, Univ. Calif., Los Angeles. 58 pp.
- MUNZ, P. A. 1974. A flora of southern California. Univ. Calif. Press, Los Angeles. 1086 pp.
- RADTKE, K. 1978. Wildland plantings & urban forestry. Native & exotic 1911–1977. Forestry Division. Co. Los Angeles Depart. For. Fire Warden. 134 pp.
- SCHULMAN, E. 1947. Tree-ring hydrology in southern California. *Lab. Tree-Ring Res., Bull. No. 4*. 36 pp.
- SWANSON, C. J. 1967. The ecology and distribution of *Juglans californica* in southern California. M.A. thesis, Calif. State Univ., Los Angeles. 115 pp.
- THOMSEN, H. H. 1963. *Juglans hindsii*, the central California black walnut, native or introduced? *Madroño* 17:1–10.

(Received 18 Jan 1990; revision accepted 30 Aug 1990.)

## ANNOUNCEMENT

### CHANGE IN SUBSCRIPTION RATE FOR *MADROÑO*

The Council of the California Botanical Society has voted to increase the institutional subscription rate for *Madroño* to \$50.00 per year. Individual (\$22.00), student (\$12.00), and family (\$25.00) membership dues for the California Botanical Society are unchanged.



# HABITAT RELATIONSHIPS OF THE PACIFIC COAST SHRUB *OEMLERIA CERASIFORMIS* (ROSACEAE)

JOSEPH A. ANTOS and GERALDINE A. ALLEN  
Department of Biology, University of Victoria,  
Victoria, British Columbia, V8W 2Y2, Canada

## ABSTRACT

*Oemleria cerasiformis* is a common shrub in parts of the Pacific Northwest, but little is known about its autecology. To examine the habitat relationships of this species, we sampled 56 stands representing most of its geographical range. These stands contained a diverse array of woody species, indicating considerable variation in the habitats occupied. DCA ordinations for all stands and for various subsets indicated that moisture, disturbance, and phytogeographical patterns are important variables among stands. Both in the Willamette Valley, Oregon, and on southeastern Vancouver Island, B.C. (areas where it is common), *O. cerasiformis* occurs along a moisture gradient from *Quercus garryana* woods through *Pseudotsuga menziesii* forests to streamside groves of *Alnus rubra*. In areas too dry for growth on uplands and in areas of wet coniferous forest, *O. cerasiformis* occurs primarily along streams. It is common on upland sites only in the narrow segment of the regional moisture gradient that spans the transition from *Q. garryana* to *P. menziesii* forests.

*Oemleria cerasiformis* (Hook. & Arn.) Landon (*Osmaronia cerasiformis* (Torrey & A. Gray) E. Greene), hereafter *Oemleria*, is a large shrub that occurs along the Pacific coast of North America. The monotypic genus *Oemleria* is similar to *Prunus* in many respects, but is dioecious and has multiple pistils per flower. It blooms in February or March over most of its range. Both sexes have racemes of small white flowers. Males and females differ somewhat in flowering phenology (Allen 1986), and the males on average produce more flowers than the females (Allen and Antos 1988). The fruits are drupes (much like those of *Prunus*) and ripen in May or June, and each of the five pistils in a female flower can produce a fruit.

*Oemleria* leafs out in February to March (sooner than most associated deciduous shrubs), and forms few new leaves after May. The leaves are generally retained until autumn, but on drier sites 50% or more of the leaves can be shed during dry periods in July and August.

Individual plants can grow to 7 m in height, and can form large clumps with ten or more closely spaced stems. The plants do not spread via rhizomes or root sprouts, but layering of stems may occasionally give rise to new clumps. Layering is rare, except in old forests where plants are sometimes bent over by falling trees.

*Oemleria* occurs west of the Cascade Range and the Sierra Nevada from southwestern British Columbia to central California, and is



most common from central Oregon northward. To the south it becomes more restricted to wet habitats. Populations generally have male-biased sex ratios (Allen and Antos 1988), but we have found no niche differences between sexes (Allen and Antos unpubl.).

Little information is available on the habitat requirements of *Oemleria*. In conjunction with a study of sex ratios (Allen and Antos, unpublished data), we determined the species composition of stands containing *Oemleria* throughout much of its range. In this paper we present these results, and make inferences from them about the ecological requirements of *Oemleria*.

## METHODS

We examined potential sample sites throughout the range of *Oemleria* (Fig. 1), and sampled wherever it was reasonably abundant. Sampling was concentrated in the Willamette Valley of Oregon and on Vancouver Island, B.C., areas where *Oemleria* is especially common. We chose sites to encompass as much of the variation in habitats of *Oemleria* as possible. Sites were sampled if they (1) contained 100 or more mature individuals (enough to obtain a good estimate of sex ratio) and (2) were fairly homogeneous with respect to topography and vegetation. We relaxed the first criterion occasionally in habitats where it was difficult to find large populations. *Oemleria* often occurs in ecotones (e.g., margins of woods) and in patchy habitat mosaics. Thus the areas sampled were variable in size, and often irregular in shape.

At each site, we first examined *Oemleria* plants to determine the sex ratio and then recorded habitat characteristics for the area circumscribed by these plants. We visually estimated canopy cover for each woody species within the area, as well as total cover of trees, tall shrubs and low shrubs. Herbaceous plants were excluded because we sampled when *Oemleria* was in bloom, prior to the emergence of many herbaceous species. We also made observations on site characteristics, stand structure, and probable past disturbances.

To examine patterns of variation among sites, we produced ordinations using Detrended Correspondence Analysis (Hill and Gauch 1980). We included cover data for all taxa present in more than two sites. All cover values were log transformed. Ordinations were obtained for (1) all sites, (2) sites on Vancouver Island, and (3) sites in the Willamette Valley. To aid in interpretation of ordination axes, we examined species patterns plotted on the ordinations.

Nomenclature follows Hitchcock and Cronquist (1973) or Munz (1973).

## RESULTS

*All sites.* Stands from different geographical regions differed in average composition (Table 1), and were generally separated on the



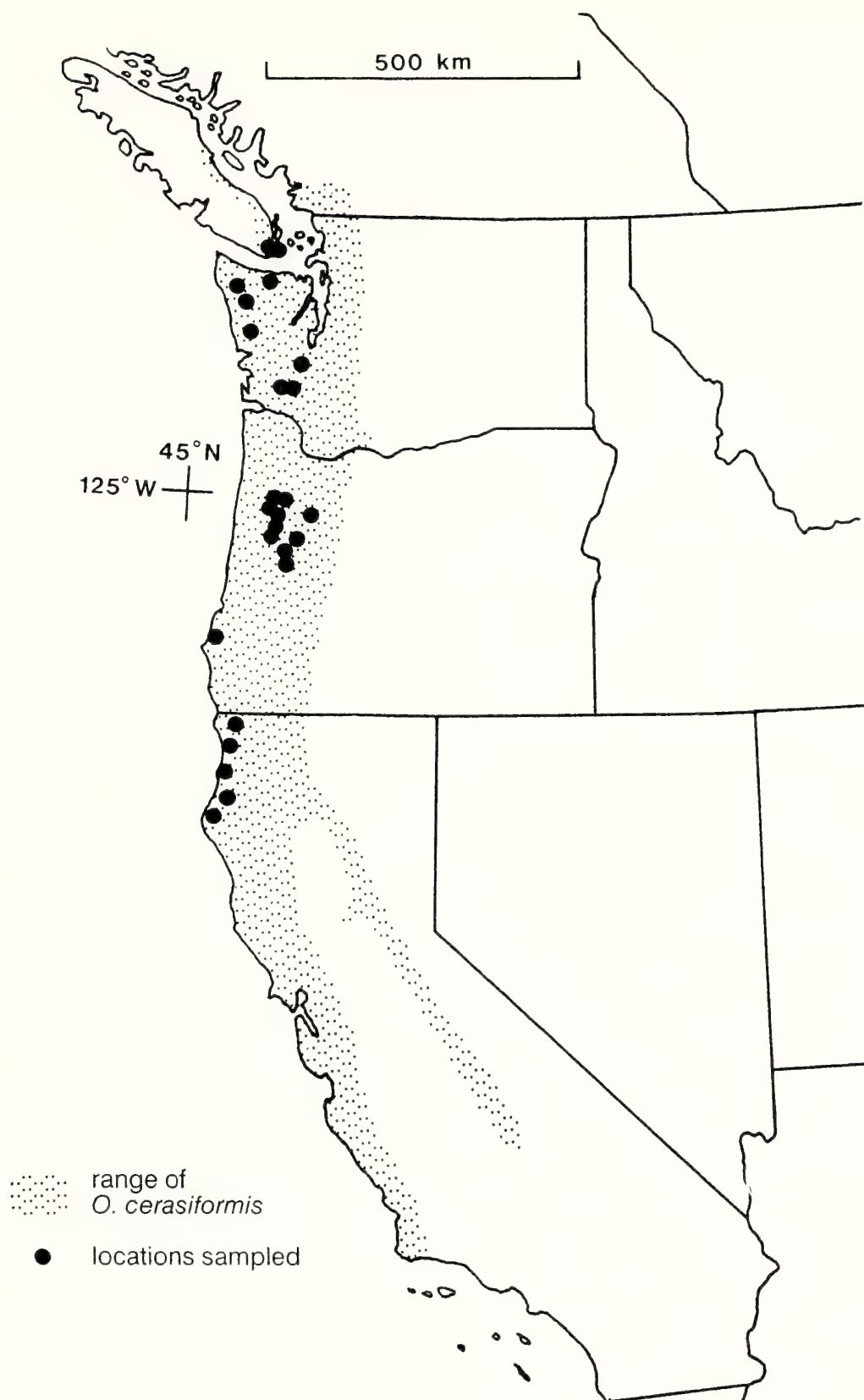


FIG. 1. Map of western North America showing the approximate range of *Oemleria cerasiformis* (stippled area) and locations sampled (black circles). Some circles, especially in the Willamette Valley and on Vancouver Island, represent more than one population sampled in the same general area.



TABLE 1. SPECIES GROWING IN STANDS CONTAINING *OEMLERIA CERASIFORMIS* BY GEOGRAPHICAL REGION. Cover is the mean percentage for all stands in a category; constancy is the percentage of stands in which a species was present. Only species that had at least 1% cover and 50% constancy in one region are included.

|                                 | Vancouver Island<br>n = 20 |      | Washington<br>n = 9 |      | Willamette Valley<br>n = 21 |      | California and<br>Southern Oregon<br>n = 6 |      |
|---------------------------------|----------------------------|------|---------------------|------|-----------------------------|------|--|------|
|                                 | Cover                      | Con. | Cover               | Con. | Cover                       | Con. | Cover                                      | Con. |
| Trees                           |                            |      |                     |      |                             |      |  |      |
| <i>Abies grandis</i>            | 7.6                        | 70   | 2.2                 | 11   | 1.0                         | 67   | 2.5  | 33   |
| <i>Acer macrophyllum</i>        | 14.8                       | 70   | 8.6                 | 67   | 24.4                        | 90   | 7.5  | 83   |
| <i>Alnus rubra</i>              | 10.3                       | 35   | 38.5                | 89   | 10.3                        | 43   | 31.7                                       | 100  |
| <i>Crataegus</i> spp.           | 1.0                        | 50   | 0                   | 0    | 1.7                         | 67   | 0  | 0    |
| <i>Fraxinus latifolia</i>       | 0                          | 0    | 3.7                 | 11   | 9.2                         | 76   | 0  | 0    |
| <i>Lithocarpus densiflorus</i>  | 0                          | 0    | 0                   | 0    | 0                           | 0    | 5.0  | 50   |
| <i>Picea sitchensis</i>         | 0                          | 0    | 8.9                 | 67   | 0                           | 0    | 10.0                                       | 50   |
| <i>Populus trichocarpa</i>      | 0.6                        | 15   | 5.3                 | 56   | 2.7                         | 57   | 14.2                                       | 17   |
| <i>Prunus avium</i>             | 0.4                        | 25   | 0                   | 0    | 1.7                         | 62   | 0  | 0    |
| <i>Pseudotsuga menziesii</i>    | 32.0                       | 65   | 5.7                 | 56   | 16.7                        | 86   | 17.5                                       | 67   |
| <i>Quercus garryana</i>         | 18.8                       | 50   | 0                   | 0    | 12.7                        | 71   | 0  | 0    |
| <i>Rhamnus purshiana</i>        | 2.8                        | 75   | 0.3                 | 22   | 1.9                         | 76   | 4.1  | 67   |
| <i>Salix</i> spp.               | 1.0                        | 15   | 1.2                 | 56   | 0.1                         | 14   | 12.3                                       | 83   |
| <i>Sequoia sempervirens</i>     | 0                          | 0    | 0                   | 0    | 0                           | 0    | 5.8  | 50   |
| <i>Thuja plicata</i>            | 5.2                        | 50   | 1.4                 | 44   | 0.4                         | 14   | 0  | 0    |
| <i>Tsuga heterophylla</i>       | 0.1                        | 5    | 1.6                 | 56   | 0.1                         | 14   | 0  | 0    |
| <i>Umbellularia californica</i> | 0                          | 0    | 0                   | 0    | 0                           | 0    | 3.3  | 50   |



TABLE 1. Continued.

|                              | Vancouver Island<br>n = 20 |      | Washington<br>n = 9 |      | Willamette Valley<br>n = 21 |      | California and<br>Southern Oregon<br>n = 6 |      |
|------------------------------|----------------------------|------|---------------------|------|-----------------------------|------|--|------|
|                              | Cover                      | Con. | Cover               | Con. | Cover                       | Con. | Cover                                      | Con. |
| Shrubs                       |                            |      |                     |      |                             |      |  |      |
| <i>Acer circinatum</i>       | 0                          | 0    | 11.0                | 78   | 15.8                        | 62   | 0  | 0    |
| <i>Amelanchier alnifolia</i> | 0.8                        | 30   | 0.1                 | 11   | 1.5                         | 57   | 0  | 0    |
| <i>Berberis nervosa</i>      | 3.6                        | 55   | 0.1                 | 11   | 0.3                         | 10   | 0.8  | 17   |
| <i>Corylus cornuta</i>       | 0.3                        | 10   | 0.2                 | 11   | 19.4                        | 95   | 0.3  | 17   |
| <i>Gaultheria shallon</i>    | 2.0                        | 15   | 2.1                 | 56   | 0.3                         | 14   | 0  | 0    |
| <i>Holodiscus discolor</i>   | 6.5                        | 65   | 0.9                 | 11   | 1.9                         | 76   | 7.5  | 33   |
| <i>Ilex aquifolium</i>       | 1.5                        | 55   | 0.1                 | 11   | 0                           | 0    | 0  | 0    |
| <i>Philadelphus lewisii</i>  | 0.7                        | 20   | 0                   | 0    | 1.0                         | 57   | 0  | 0    |
| <i>Physocarpus capitatus</i> | 0.7                        | 20   | 0.9                 | 11   | 1.7                         | 57   | 0  | 0    |
| <i>Rhus diversiloba</i>      | 0                          | 0    | 0                   | 0    | 5.5                         | 52   | 1.7  | 17   |
| <i>Rubus discolor</i>        | 2.0                        | 60   | 0.6                 | 11   | 9.0                         | 81   | 0  | 0    |
| <i>Rubus parviflorus</i>     | 0.1                        | 10   | 1.7                 | 44   | 0.9                         | 38   | 10.8                                       | 83   |
| <i>Rubus spectabilis</i>     | 3.8                        | 20   | 21.8                | 89   | 3.0                         | 29   | 18.3                                       | 50   |
| <i>Rubus ursinus</i>         | 5.1                        | 80   | 0.2                 | 11   | 5.3                         | 86   | 40.8                                       | 100  |
| <i>Sambucus racemosa</i>     | 0.3                        | 15   | 6.3                 | 78   | 0.4                         | 29   | 25.8                                       | 50   |
| <i>Symphoricarpos albus</i>  | 36.8                       | 100  | 7.1                 | 67   | 30.0                        | 100  | 0  | 0    |
| <i>Vaccinium ovatum</i>      | 0                          | 0    | 0                   | 0    | 0                           | 0    | 5.2  | 50   |



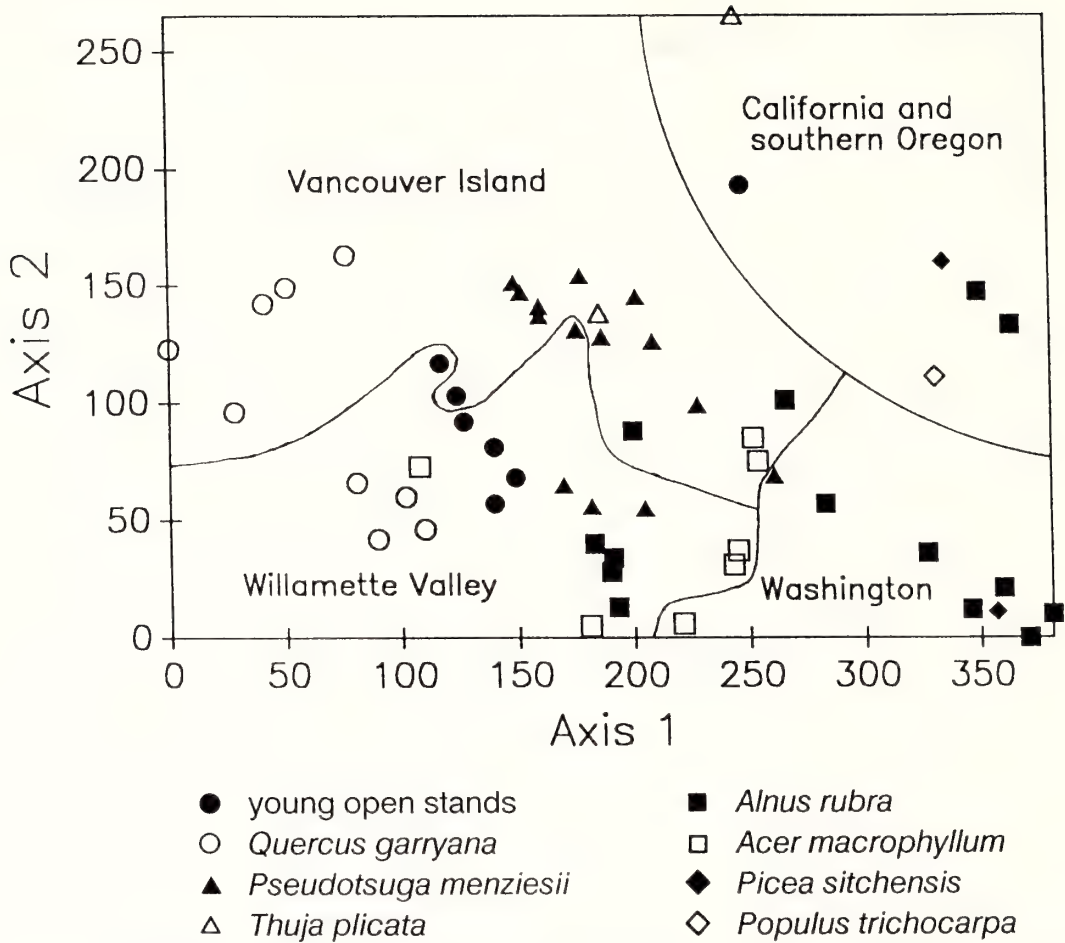


FIG. 2. Ordination (axes 1 and 2) from Detrended Correspondence Analysis for all 56 stands. The lines separate stands from different geographical regions. The symbols indicate the most abundant (highest cover) tree species at the forested sites.

ordination (Fig. 2). Two patterns are apparent: a moisture gradient related to exposure to Pacific storms, and a north-south floristic gradient. Relatively dry *Quercus garryana* stands were on the left side of the first axis, wet *Alnus rubra* stands were on the right side, and *Pseudotsuga menziesii* stands occupied the center (Fig. 2).

Although moisture generally increases to the north in the study area, the stands did not separate out in a simple north-south pattern (Fig. 2). Dry-site species such as *Quercus garryana* and *Symphoricarpos albus* were common in stands from the Willamette Valley and from Vancouver Island (Table 1), which are sheltered by the Oregon Coast Range or the Olympic and Vancouver Island Mountains. In contrast, the wetter-site species, *Picea sitchensis* and *Rubus spectabilis* occurred primarily in the Washington and California stands, which are directly exposed to storms from the Pacific.

The non-forest stands, most of which were in early stages of succession to forest, were located on the ordination primarily between the dry *Quercus* stands and the wetter stands containing conifers, *Acer macrophyllum*, or *Alnus rubra*. The location of non-forest stands toward the drier end of the moisture gradient represented by the



first ordination axis is related to the presence of species characteristic of open habitats.

The second ordination axis in Fig. 2 reflected phytogeographical patterns. *Acer circinatum* and *Fraxinus latifolia* occur in the Willamette Valley and Washington stands but are absent from the other stands (Table 1), which may explain why stands from both the north and south ends of the study area occurred at the top of the ordination. The stands sampled span a long north-south gradient, and along this gradient many species reach range limits or change drastically in abundance.

In order to reveal underlying patterns that might be obscured by the strong phytogeographical gradient in the overall data set, we examined different geographic areas separately. For the two areas for which we had concentrations of 20 or more sample stands, we performed separate ordinations.

*Vancouver Island.* The stands sampled were all on the extreme southeast end of the island, which is the driest part. *Oemleria* is abundant in a variety of habitats in this area, but is uncommon elsewhere on the island. The ordination of the 20 stands from Vancouver Island indicated one major gradient, a moisture gradient from dry *Quercus* stands to wet *Alnus* stands (Fig. 3). The *Quercus* stands clustered on the right side of the ordination; they generally had deep soils, often with a high cover of *Oemleria* and *Symphoricarpos albus*. The driest *Quercus* stands in the area, which occurred on shallow soils over bedrock, supported few or no *Oemleria*. The *Quercus* forests grade into moderately dry coniferous forest dominated by *Pseudotsuga menziesii*. *Oemleria* is often the most common tall shrub species in these forests. Most forests on Vancouver Island are wetter than those containing *Oemleria* and would extend along the moisture gradient off to the left side of the ordination.

*Washington.* The stands sampled in Washington generally had *Alnus rubra* as the dominant canopy tree, and shrubs typical of wet sites, especially *Rubus spectabilis*, were common (Table 1). These sites were wet enough to support dense coniferous forest but had undergone human disturbance or were on stream bottoms where the vegetation is naturally disturbed by alluvial activity. *Oemleria* occurs in some very old riparian rainforests on the Olympic Peninsula.

*Willamette Valley.* In Oregon, *Oemleria* is common in the Willamette Valley and occurs along streams far into the surrounding mountains. It is much less common along the coast, where it occurs on sites similar to those sampled in Washington. Sampling was concentrated in the Willamette Valley and adjacent parts of the Cascade and Coastal Mountains. The first axis of the ordination of Willamette Valley sites represented a moisture gradient from *Quercus garryana* forests on the valley bottom to *Acer macrophyllum*–



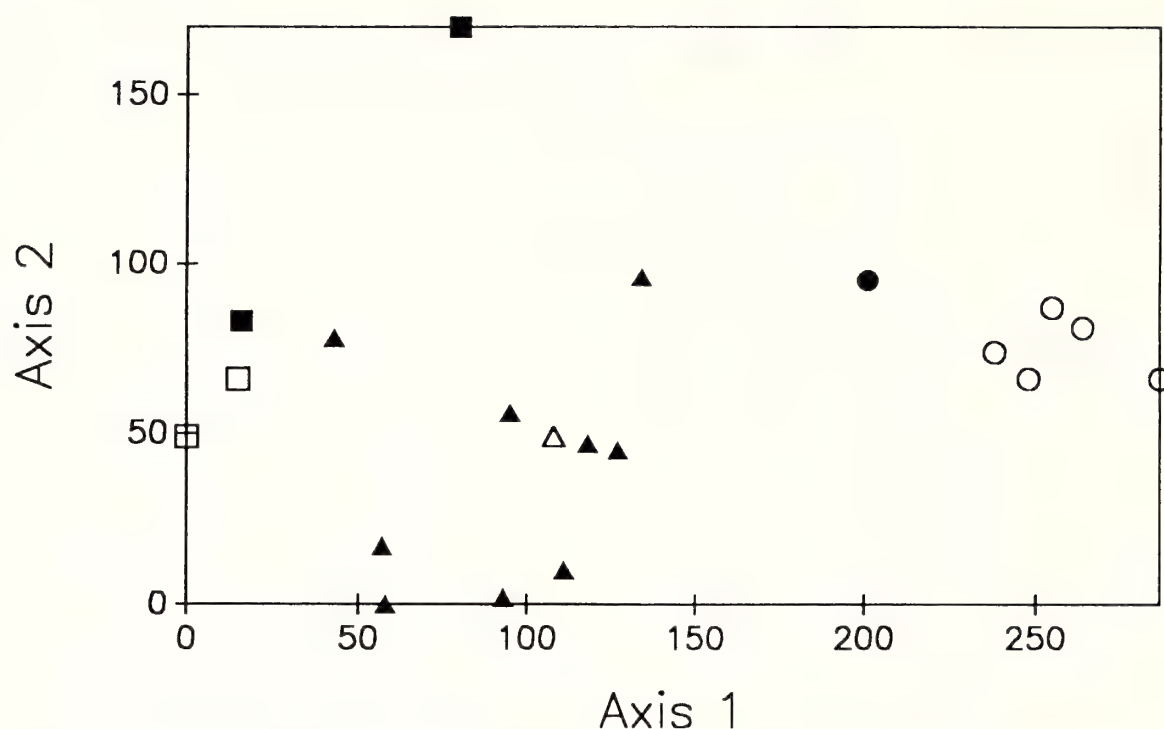


FIG. 3. Ordination (axes 1 and 2) from Detrended Correspondence Analysis of 20 stands on Vancouver Island. Symbols as in Fig. 2.

*Alnus rubra* forests along mountain streams (Fig. 4). The second axis represented a gradient from streamside *Alnus rubra* forests, often with considerable *Fraxinus latifolia*, to well drained *Pseudotsuga menziesii* forests. The open sites, in the upper left region of the ordination (Fig. 4), were mostly abandoned pastures with scattered old trees and a few young trees and shrubs.

Although *Oemleria* is common in the Willamette Valley, especially along streams, it is virtually absent from many types of sites. It is common in *Quercus garryana* forests on alluvial bottoms, but rare on very wet sites dominated by *Fraxinus latifolia*. It occurs in some upland *Quercus* and *Pseudotsuga* forests adjacent to the Willamette Valley. However, it is found primarily in wetter microsites within these forests, so many of these forests may be too dry to support *Oemleria*. Farther into the mountains, *Oemleria* is generally confined to relatively open streamside forests.

*Southern sites.* The six southernmost stands sampled did not clump tightly on the ordination of all sites (Fig. 2), and they varied considerably in composition. They were all near the coast (one in southern Oregon and five in California) and were fairly wet, as indicated by the high cover and consistent occurrence of *Alnus rubra* (Table 1). Other species present, such as *Picea sitchensis*, *Sequoia sempervirens*, and *Rubus spectabilis*, also indicate wet sites. Most of these stands had been affected in the past by human disturbances (primarily logging). In the *Sequoia* zone, *Oemleria* can be locally com-



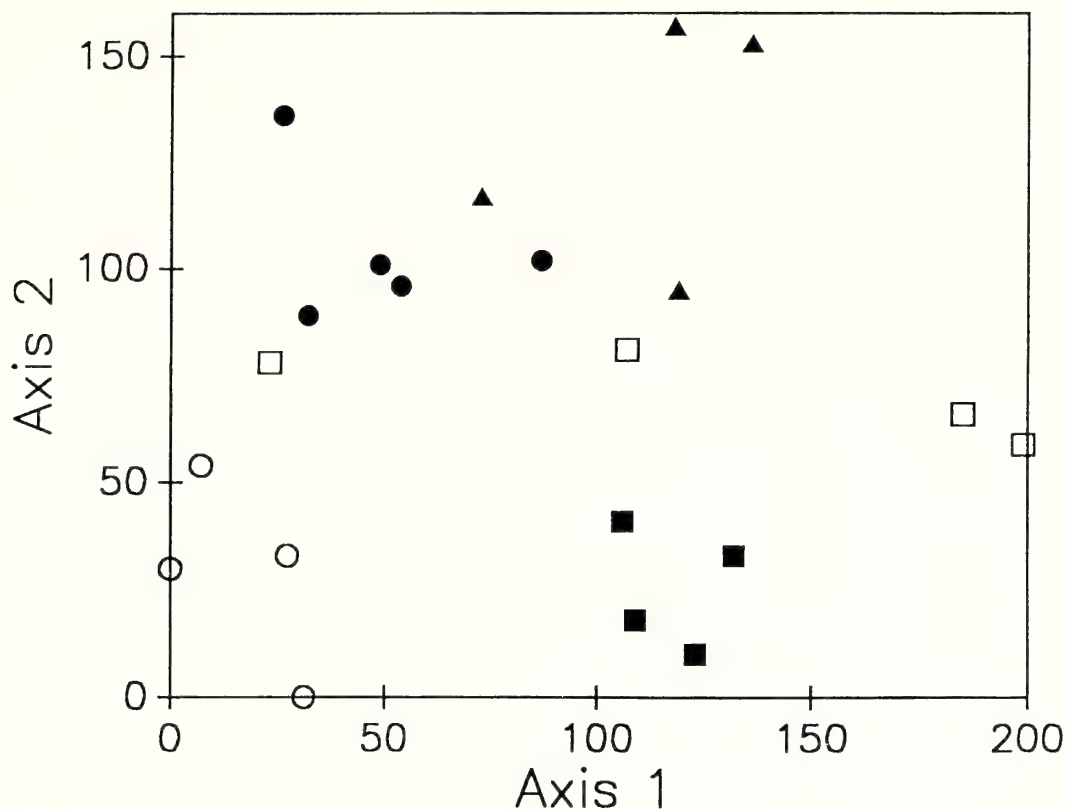


FIG. 4. Ordination (axes 1 and 2) from Detrended Correspondence Analysis of 21 stands in the Willamette Valley. Symbols as in Fig. 2.

mon along streams where the tree canopy remains open, but it is generally absent in upland forests.

*Oemleria* also occurs inland from the coastal *Sequoia* zone and south to approximately Santa Barbara, but it is rare and no sites were sampled. It occurs in the Sierra Nevada south to Tulare County. In the South Coast Ranges we have observed it in alluvial *Sequoia* forests near the coast and in mixed evergreen hardwood forests along streams farther inland.

#### DISCUSSION

*Oemleria* occurs along the Pacific Coast over a distance of 1700 km, but does not extend east of the Cascade Range or the Sierra Nevada. It is most common at low elevations; all stands sampled were below 250 m elevation. *Oemleria* is usually found at low elevations in the northern parts of its range, but can occur at elevations up to 1500 m in California. Thus the plants are generally found in a fairly mild maritime climate.

Although *Oemleria* was the most abundant shrub in some of the forests stands that we sampled, it is uncommon over much of its geographical range and is often restricted to specific types of habitats. In the south, *Oemleria* is rare primarily because most of the landscape is too dry to support it, and it occurs along streams or in other



moist locations. Even as far north as Vancouver Island there are sites too dry for *Oemleria*, as indicated by abrupt edges of populations along rocky areas with stunted *Quercus garryana*. We have observed dieback and mortality of *O. cerasiformis* on some *Quercus* sites in British Columbia during dry years. In most of western Washington and coastal Oregon, *Oemleria* occurs along streams in a matrix of wet coniferous forests. It is generally absent from upland sites wet enough to support *Tsuga heterophylla* forest. Thus the abundance of *Oemleria* is greatly limited in the northern part of its range, where wet coniferous forests cover much of the landscape. Its occurrence along streams is probably related to chronic disturbance resulting from alluvial activity. Throughout much of its range, *Oemleria* extends along streams into both wetter and drier areas than it normally occupies in upland vegetation.

Lack of moisture is unlikely to be the reason for the absence of *Oemleria* from wet, upland coniferous forests. The plants are probably unable to survive in the low light environment under dense coniferous canopies. Although *Oemleria* is moderately shade tolerant and grows well under *Quercus garryana* and in open stands of *Pseudotsuga menziesii*, we frequently observed plants dying back (apparently from lack of light) when overtopped by *Abies grandis* or *Thuja plicata*. It is also possible that the soils of wet, upland coniferous forests are unfavorable for *Oemleria*, which normally grows on relatively rich alluvial soils or on soils that developed under hardwood forests or savanna. Many of the *Pseudotsuga* forests in which *Oemleria* grows have developed from *Quercus* woodlands in historic times, as a result of fire suppression.

*Oemleria* reaches its greatest regional abundance in areas where it grows on upland sites spanning the transition from *Quercus garryana* to *Pseudotsuga menziesii* forests. The abundance of *Oemleria* in the Willamette Valley of Oregon reflects the large areas of such habitat. These areas previously supported fire-maintained *Quercus* savanna or woodland, which has now become *Quercus* or *Pseudotsuga* forest (Franklin and Dyrness 1973; Thilenius 1968). *Oemleria* occurs in *Pseudotsuga* forests that have developed on former prairie sites in Washington (Franklin and Dyrness 1973). In northern California, *Oemleria* sometimes grows with *Quercus garryana* above the fog belt in woodlands that are more similar to those in the Willamette Valley than to other *Quercus* woodlands in California (Sugihara et al. 1987).

Young *Oemleria* plants are most frequent in partially disturbed areas, e.g., under scattered trees in abandoned pastures or along forest margins. First year seedlings can be abundant in forests but seem to rarely survive long except in openings. Even-aged populations are uncommon, and *Oemleria* does not appear to invade open sites rapidly. Young plants usually occur beneath old plants. Seed-



lings can establish in open grassy areas, but they usually do so in very low density.

*Oemleria* can be very long-lived. The plants frequently die back when conditions are adverse but often resprout from the base, which may allow them to persist longer under low light conditions, as observed for *Prunus serotina* (Auclair and Cottam 1971). In relatively open forests along streams, *Oemleria* populations can persist because of the occasional establishment of new plants on disturbed microsites and the low mortality rates of shrubs that may pass through multiple generations of stems.

Historically, individual *Oemleria* plants probably were adversely affected by frequent fires because of their thin bark and large size. Fire suppression, which initially may have led to density increases in *Oemleria* populations, also results in succession to coniferous forests, which has probably eliminated populations on some sites. *Pseudotsuga menziesii* can form fairly dense stands on sites too dry for *Oemleria*. If the same processes restricting *Oemleria* in wet coniferous forests also operate in the drier coniferous forests that can develop from *Quercus* woodlands, the species may decrease in abundance on upland sites. Factors that prevent the development of dense coniferous forests, including fires in the past and some forms of human disturbance at present, are important in maintaining the abundance of *Oemleria* on uplands.

In summary, it appears that the local abundance and overall geographical distribution of *Oemleria* are related to: (1) a restriction to a fairly mild, maritime climate, (2) a moisture requirement that restricts its distribution to moist areas over much of its range, (3) an inability to tolerate either low light levels or soil conditions in wet, upland coniferous forests, which greatly restricts its distribution and abundance in the northern part of its range, and (4) a need for some disturbance of the vegetation to allow seedling establishment. Thus, *O. cerasiformis* occurs along streams over a large geographic area, but occurs on upland sites only on a narrow segment of the regional moisture gradient.

#### ACKNOWLEDGMENTS

We thank Jennifer Allen and Terri Suttill for help with field work, and the curators of UC, JEPS, CAS, DAV, OSC, WTU, and V for access to specimens. This work was funded by the Natural Sciences and Engineering Research Council of Canada.

#### LITERATURE CITED

- ALLEN, G. A. 1986. Flowering pattern and fruit production in the dioecious shrub *Oemleria cerasiformis* (Rosaceae). *Canad. J. Bot.* 64:1216–1220.
- and J. A. ANTOS. 1988. Relative reproductive effort in males and females of the dioecious shrub *Oemleria cerasiformis*. *Oecologia* 76:111–118.
- AUCLAIR, A. N. and G. COTTAM. 1971. Dynamics of black cherry (*Prunus serotina* Ehrh.) in southern Wisconsin. *Ecol. Monogr.* 41:153–177.



- FRANKLIN, J. F. and C. T. DYRNESS. 1973. Natural vegetation of Oregon and Washington. U.S.D.A. Forest Serv. Gen. Tech. Rept. PNW-8.
- HILL, M. O. and H. G. GAUCH, JR. 1980. Detrended correspondence analysis: an improved ordination technique. *Vegetatio* 42:47--58.
- HITCHCOCK, C. L. and A. CRONQUIST. 1973. *Flora of the Pacific Northwest*. Univ. Washington Press, Seattle.
- MUNZ, P. A. 1973. *A California flora with supplement*. Univ. California Press, Berkeley.
- SUGIHARA, N. G., L. J. REED, and J. M. LENIHAN. 1987. Vegetation of the bald hills oak woodlands, Redwood National Park, California. *Madroño* 34:192-208.
- THILENIUS, J. F. 1968. The *Quercus garryana* forests of the Willamette Valley, Oregon. *Ecology* 49:1124-1133.

(Received 2 Jan 1990; revision accepted 6 Aug 1990.)

## ANNOUNCEMENTS

### NEW PUBLICATIONS

ALCOCK, JOHN. *Sonoran desert summer*. University of Arizona Press, 1615 E. Speedway, Tucson, Arizona 85719, 1990, x, [i], 187, [1] pp., illus., ISBN 0-8165-1150-0 (hardbound), price unknown. [A series of 37 bot. and esp. zool. vignettes for May through Sep.]

EVENS, JULES G. *The natural history of the Point Reyes Peninsula*. National Seashore Association, Point Reyes, California 94956, 1988, xiii, 226 pp., illus. (B&W exc. color cover), ISBN 0-911235-02-7 (paperbound), \$14.95. [With 7 chapters on climate, geology, flora, fauna, incl. 5 species lists, of this famous area in Marin Co., California. For review see G. M. Fellers, *Wildflower* 2(2): 28-29.]

MURRAY, DAVID F. and ROBERT LIPKIN. *Candidate threatened and endangered plants of Alaska, with comments on other rare plants*. University of Alaska Museum, Fairbanks, Alaska, 1987, 75, [1] pp., illus., ISBN 0-931163-03-X (spiral bound), price unknown. [On 17 threatened, endangered, and 18 rare spp.]

WAGNER, WARREN L., DERRAL R. HERBST and S. H. SOHMER. *Manual of the flowering plants of Hawai'i*. 2 vols. University of Hawaii Press, 2840 Kolowau St., Honolulu, Hawaii 96822, winter 1990, xviii, vi, 1853, [1] pp., 1 pl. (color fp.), B&W text illus., endpaper maps, ISBN 0-8248-1152-6 (hardbound), \$85.00. [Contents: *vol. 1*: intro.; methods and scope; geol.; climate; veg.; important collections; abbr.; tax. treatment (phyletic list fam. in Hawaii, keys to higher order taxa; Acanth. to Nyctagin.); *vol. 2*: tax. treatment (Ochn. to Zygophyll., monocotyledons); glossary; biblio.; addendum on *Melicope* (Rut.); illus. vouchers; index.]



DISTRIBUTION, ECOLOGY, AND TAXONOMY OF  
*ERYTHRONIUM* (LILIACEAE) IN THE  
SIERRA NEVADA OF CALIFORNIA

JAMES R. SHEVOCK

Department of Botany, California Academy of Sciences,  
San Francisco, CA 94118-4599

JIM A. BARTEL

Office of Endangered Species, U.S. Fish and Wildlife Service,  
2800 Cottage Way, Sacramento, CA 95825-1846

GERALDINE A. ALLEN

Department of Biology, University of Victoria,  
Victoria, British Columbia V8W 2Y2, Canada

ABSTRACT

Five species of *Erythronium* occur in the Sierra Nevada of California. A new species, *E. pluriflorum*, endemic to the south-central portion of the range, is described and illustrated. *Erythronium pusaterii* is elevated to the rank of species from *E. grandiflorum* and represents the most southern occurrence of the genus for western North America. Distribution and habitat preferences are discussed, and a key for Sierran *Erythronium* is also provided.

Approximately 25 species of *Erythronium* range from southern Europe and temperate Asia to the Atlantic and Pacific coasts of North America (Willis 1973). The evolutionary relationships within the genus are not well understood. There appear to be two major groupings of species (perhaps corresponding to subgenera) which have not been formally recognized. One of these includes the eastern North American and Old World species, and the other includes the species of western North America. Of the 18 species in North America (Kartesz and Kartesz 1980), 13 species are recorded for California (Munz and Keck 1959; Munz 1968). The greatest species diversity for the genus occurs in the northwest portion of the California Floristic Province (Applegate 1935; Allen and Antos 1988).

The taxonomy of Sierran *Erythronium* has remained essentially unchanged since Applegate's 1935 monograph of western North American species, except for the addition of *E. grandiflorum* Pursh subsp. *pusaterii* described by Munz and Howell in 1964 (recognized herein as *E. pusaterii*). The major key division for west American *Erythronium* is based on presence/absence of mottled leaves. All Sierran *Erythronium* species are diploid,  $n=12$ ,  $2n=24$  (Cave 1970 and counts by the third author).



*Distribution.* The Sierra Nevada contains five species of *Erythronium* that are primarily restricted to this mountain range. Three species are rare and highly localized in distribution. *Erythronium multiscapoideum* (Kellogg) A. Nelson & P. B. Kennedy and *E. purpurascens* S. Watson are more wide-ranging species that venture northward into the southernmost extension of the Cascade Range in Shasta County. Alpine, Calaveras, Fresno, Inyo, Kern, and Mono counties lack a confirmed occurrence for the genus in the Sierra Nevada (Fig. 1).

The northern Sierra Nevada contains three *Erythronium* species. *Erythronium purpurascens* occupies montane habitats between 1200–2450 m from Shasta County south to Tuolumne County (floristic works attributing this species to the southern Sierra Nevada of Tulare County are erroneous). The other two species, *E. multiscapoideum* and *E. tuolumnense* Applegate, occupy foothill woodland habitats generally below 600 m. *Erythronium multiscapoideum* is the only Sierra Nevada species with mottled leaves. This species can propagate by producing new bulbs at the ends of long slender rhizomes. It is widely distributed, ranging from Shasta County south to Mariposa County, and often occurs on serpentine substrates. *Erythronium tuolumnense* is a localized, rare endemic of Tuolumne County. Although this species is also cited as occurring in Stanislaus County (Munz and Keck 1959), no herbarium specimens or populations are known from that county. Moreover, records at the California Natural Diversity Data Base, Department of Fish and Game, cite Tuolumne County for all of the known occurrences. Geographically, *E. tuolumnense* is located near the center of the Sierra Nevada (ca. 30 km west of Yosemite National Park). Populations occur primarily on north-facing slopes between 500–1160 m, mainly in *Quercus kelloggii*–*Pinus ponderosa* stands within the South Fork and Middle Fork of the Stanislaus River and North Fork of the Tuolumne River drainages. The majority of the populations occur on federal lands administered by the Stanislaus National Forest and are managed to conserve the species under Forest Service sensitive plant policy. The distance between the northern and southernmost populations is only 25 kilometers. Reproduction is largely vegetative by means of numerous closely spaced offsets that develop into additional bulbs (Applegate 1935), a feature rare in Californian *Erythronium*. *Erythronium tuolumnense* also has perianth segments with well developed saclike appendages. It appears to be a remarkable relictual species, confined now to “cold air drainage” microhabitats. Its relationship within the genus remains uncertain.

The two southern Sierran members of the genus are high montane, occurring between 2100–2840 m, and are very localized and rare. *Erythronium pluriflorum* (described herein) is endemic to Chiquito Ridge in the San Joaquin River watershed in Madera County, and



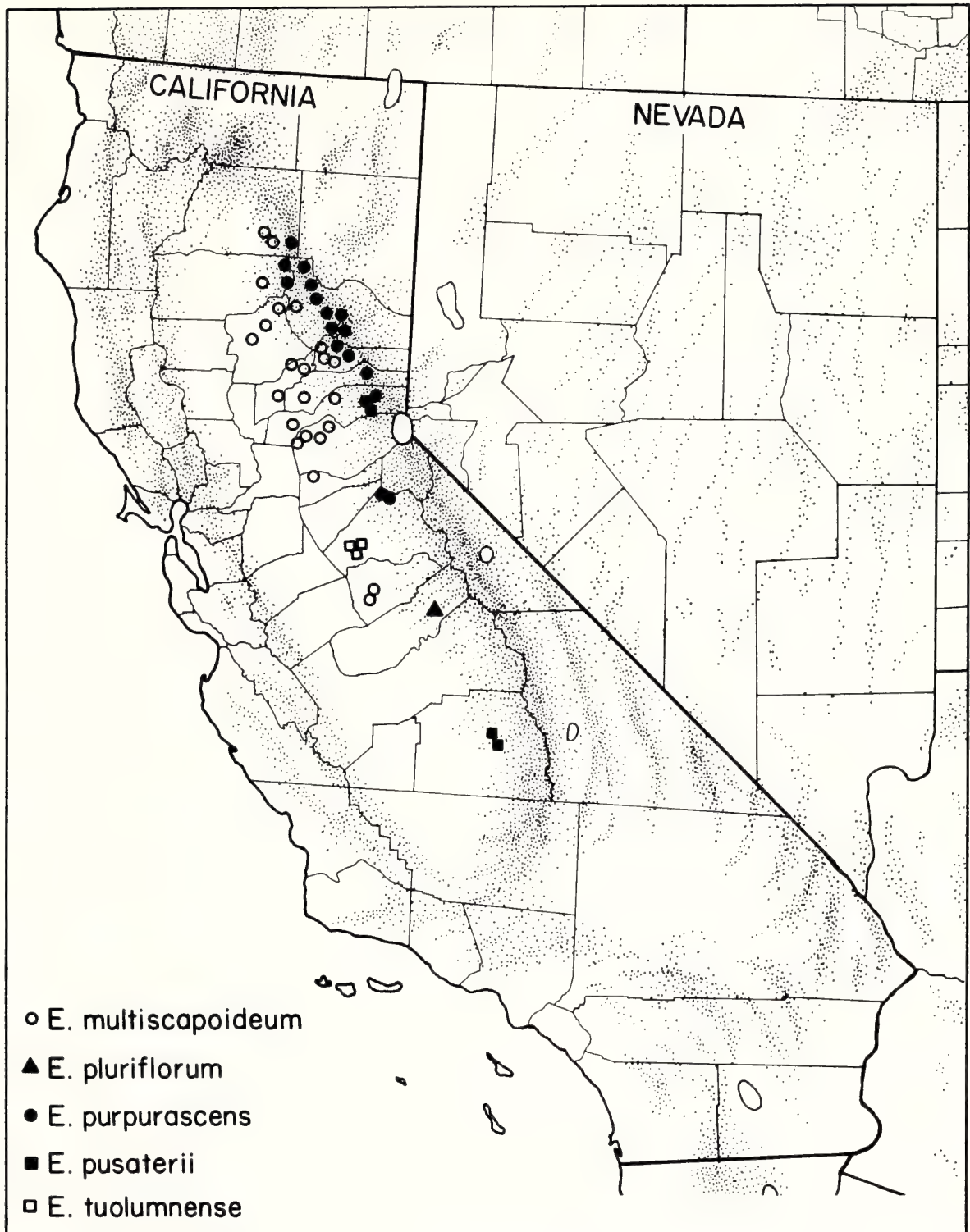


FIG. 1. Distribution of the genus *Erythronium* in the Sierra Nevada of California.

*E. pusaterii* is endemic to the Kaweah and Tule River watersheds in Tulare County (Shevock 1977). Given the number of field botanists who have collected in the Sierra Nevada this century, it is amazing that localized endemics are still being discovered and described at a relatively high rate (Shevock and Taylor 1987). This is of particular interest in regard to *E. pluriflorum*. This showy species is locally abundant within its restricted range, and road access to a large population has existed for many years.



KEY TO SIERRA NEVADA *ERYTHRONIUM*

- A. Leaves mottled; anthers cream-white; stigma plainly lobed, the lobes >1.0 mm long ..... *E. multiscapoideum*
- A' Leaves not mottled; anthers usually yellow; stigma entire or with short lobes <1.0 mm long
  - B. Perianth segments bicolored, the terminal portion cream to white, the basal portion  $\frac{1}{3}$  to  $\frac{1}{2}$  bright yellow
    - C. Perianth segments 10–15 mm long, lacking saclike appendages at base ..... *E. purpurascens*
    - C' Perianth segments 20–45 mm long, the inner three with saclike appendages at base ..... *E. pusaterii*
  - B' Perianth segments bright yellow throughout
    - D. Perianth segments 25–35 mm long, 8–12 mm wide, the inner with appendages at base; style, stigma, and filaments  $\pm$  white .... *E. tuolumnense*
    - D' Perianth segments 15–28 mm long, 4–7 mm wide, lacking saclike appendages at base; style, stigma and filaments bright yellow ..... *E. pluriflorum*

***Erythronium pusaterii*** (Munz and J. T. Howell) Shevock, Bartel and Allen, stat. & comb. nov. (Fig. 2).—*Erythronium grandiflorum* Pursh subsp. *pusaterii* Munz and J. T. Howell. Leaf. West. Bot. 10:104–105, 1964.—TYPE: USA, California, Tulare Co., along the South Fork Kaweah River below Hockett Lakes, Sequoia National Park, southern Sierra Nevada, 15 June 1964, 2560 m, *Samuel J. Pusateri s.n.* (holotype: RSA, isotype: CAS).

Bulb 5–7(–10) cm long, 1–3 cm wide. Leaves 2, unmottled, bright green with undulate margins, 20–30(–40) cm long, 3–5(–6) cm wide, oblanceolate to elliptic. Scapes 15–35(–45) cm tall, flowers, 1–5(–8), pedicels of unequal lengths. Perianth segments curved, acuminate to lanceolate, 20–45 mm long, bicolored, the terminal portion white, the basal  $\frac{1}{3}$ – $\frac{1}{2}$  bright yellow, fading pinkish after anthesis, the inner three perianth segments with saclike appendages at base. Filaments and anthers yellow; stigma with three small lobes, <1 mm long. Capsule obovoid, 25–35 mm long, 10–15 mm wide; seeds brown, elliptical in outline, flattened. Chromosome number:  $2n = 24$ .

*Exsiccatae*. USA, California, Tulare Co., from the type locality, 20 Jun 1935, *Dixon s.n.* (UC); Jun 1963, *Pusateri s.n.* (RSA); 18 Jul 1980, *Norris 100* (RSA, THRI); Moses Mountain, Jun–Jul 1895, *C. A. Purpus 1341* (UC); Moses Mountain, Golden Trout Wilderness, Sequoia National Forest, T19S, R30E, Sect. 13, 8000–9000 ft, 30 Jun 1979, *Shevock 6282* and *6286* (CAS); 13 Jul 1979, *Shevock 6336* and *6351a* (CAS); 23 Jul 1982, *Shevock 9952* (CAS, RSA); 9 Jun 1984, *MacFarlane s.n.* (CAS); 4 Jul 1982, *Holmes s.n.* (DAV); Jordan Peak, Sequoia National Forest, T20S, R31E, Sect. 15, 9100 ft, 29 Jun 1976, *Shevock 5133* (CAS, RSA); 14 Jun 1977, *Shevock 5530* (CAS, RSA, UC); 15 Jul 1982, *Shevock 9902* (CAS, FSC, RSA); Slate Mountain,  $\frac{1}{2}$  mi SW of Quaker Camp, Sequoia National Forest, T21S, R32E, Sect. 18, 7300 ft, 1 Jul 1982, *Shevock 9841* (CAS, FSC,



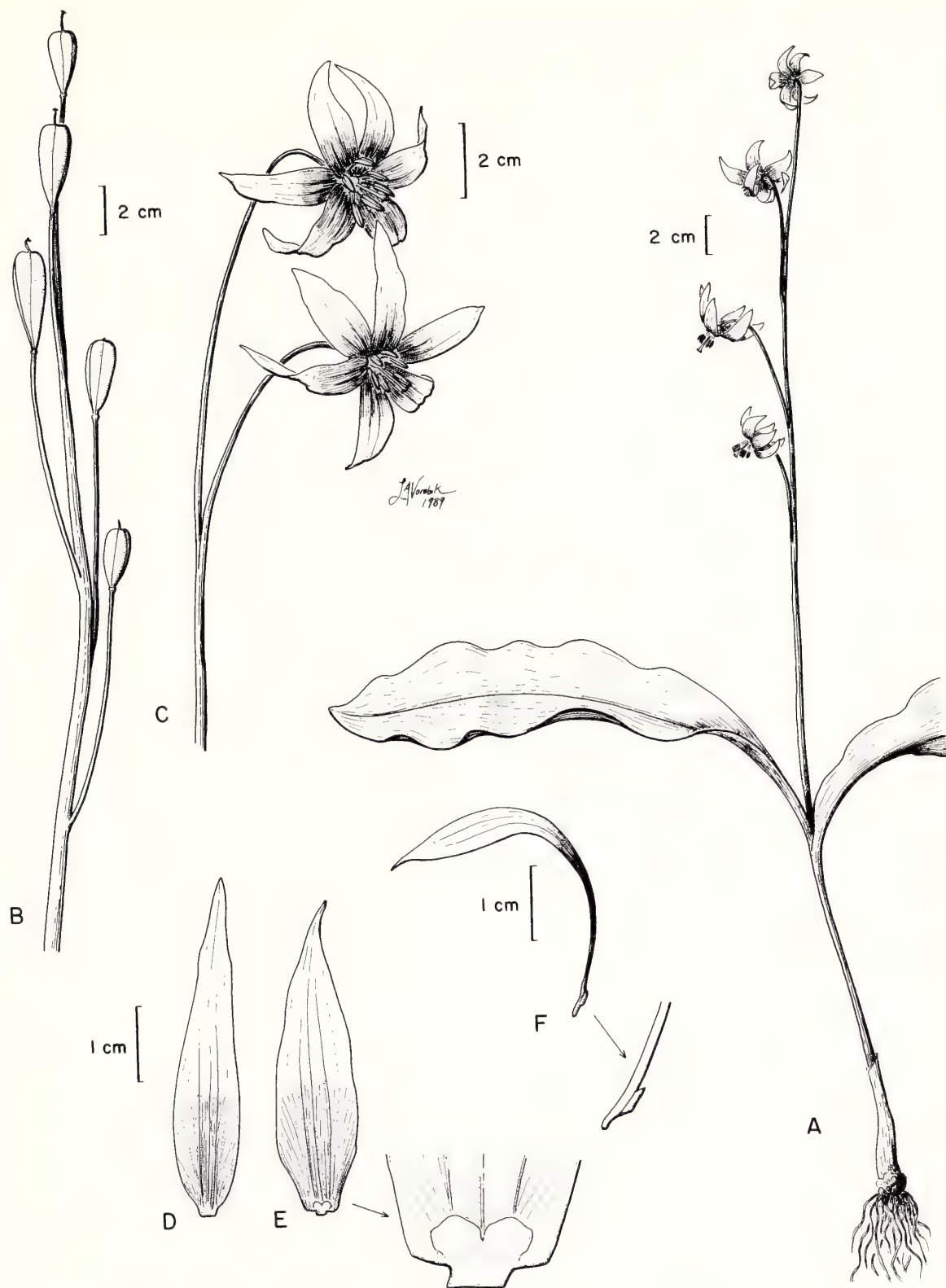


FIG. 2. *Erythronium pusaterii*. A, flowering scape; B, fruiting scape; C, close-up of flowers; D, outer perianth segment; E, inner perianth segment with saclike appendages; F, side view of perianth segment.

RSA); Slate Mountain at head of Bear Creek, T21S, R31E, Sect. 13, 8650 ft, 6 Jul 1982, Shevock 9845 (CAS, RSA, UC).

*History of the Kaweah fawn lily.* Samuel J. Pusateri was an instructor at College of the Sequoias, Visalia (Tulare County). He published the *Flora of our Sierran National Parks* in 1963. That



same year Pusateri sent to Philip Munz a photograph and a plant fragment of *Erythronium* collected along the Kaweah River near Hockett Lakes. Additional plant specimens were obtained the following year and were sent to Munz and John Thomas Howell. The Pusateri collection was obtained in June, and the description was published in September of the same year. When Munz and Howell described the “Kaweah fawn lily” in 1964, they only had two sheets of the plant along with some color transparencies. Neither Munz nor Howell had previously worked with *Erythronium*, nor were they able to observe this species in the field. Nonetheless, they correctly realized that the *Erythronium* from the South Fork of the Kaweah River was indeed a new entity.

Correspondence between Munz and Howell (attached to the isotype at CAS) indicates that their decision to include the Pusateri collection in *Erythronium grandiflorum* was based primarily on three characters: large flowers, saclike appendages at base of perianth segments, and unmottled green leaves. However, Munz and Howell (1964) noted that the range of the Tulare County material was remote from that of other forms of *E. grandiflorum*; the nearest populations of the latter are in the Yolla Bolla Mountains in Trinity County. Howell states in his letter to Philip Munz dated 30 July 1964:

“Sam Pusateri sent me two leaves and four flowers, so that I don’t have much to go on—but this material with his photos would seem to place the plant within the variation in *E. grandiflorum*. Sam has pressed the flowers so flat I am not sure if the inner segments have ‘basal appendages’ Applegate describes for the species, but I do find some flattened folds that may be remnants of these. If the appendages are present then I can see the Sierran plant only as a color variant of *E. grandiflorum* near *E. g. var. pallidum* (on account of unequal stamens). The undulate leaves are striking but can one be sure from herbarium material whether this is a noteworthy character? At the moment it seems like a variety of *grandiflorum*—but that feeling may come only from a lack of knowledge (which might come only from seeing a living plant).—Liliaceae are not easy!”.

A response from Munz (also attached to the CAS isotype) dated 7 August 1964 stated:

“On further study I agree with you about the status of Sam Pusateri’s *Erythronium* and I send you herewith a write-up hoping you can use it in the next Leaflets”.

During a review of the genus *Erythronium* for the Jepson Manual Project, the third author recognized that the Kaweah fawn lily did not belong with *E. grandiflorum*. The first author independently came to the same conclusion based on extensive observations of the plant in the field from the four known localities. Review of the



herbarium record shows that Purpus made the first collection of *E. pusaterii* in the summer of 1895. His specimen, labelled *E. purpurascens*, is the sole collection responsible for this species being cited for Tulare County in the southern Sierra Nevada (Smiley 1921; Jepson 1923; Applegate 1935; Munz and Keck 1959). *Erythronium pusaterii* was also collected by Dixon in 1935 (along the South Fork of the Kaweah River), but again, the significance of the specimen was not realized. It too was labelled *E. purpurascens*.

*Distribution, habitat and phenology.* *Erythronium pusaterii* occurs on rocky granitic or metamorphic outcrops primarily in subalpine coniferous forests of *Abies magnifica*, *Pinus murrayana* and/or *P. monticola* from 2225–2835 m. Plants form large colonies in areas where soil and humus accumulate, especially along fissures and ledges. This species is known from four localities comprising several distinct populations ranging from a few thousand individuals to several million. Flowering occurs shortly after or during snowmelt and extends from late May to mid July depending on the depth and duration of the snowpack. The distance between the northern and southernmost populations is 28 kilometers.

*Relationships.* In our view, *Erythronium pusaterii* is most closely related to the more widely distributed *E. purpurascens*, which it closely resembles except for its much larger size and the presence of saclike appendages on the inner perianth segments. Both species are high montane with several bicolored flowers per scape, and the flowers are very similar in color. The perianth segments of *E. pusaterii* are generally two to three times as large as those of *E. purpurascens*. *Erythronium purpurascens*, described by Sereno Watson in 1877, was the only montane species recorded for the Sierra Nevada at the time of the Purpus collection in 1895. Applegate (1935), who prepared a monograph of *Erythronium* in western North America, cited the Purpus collection as belonging to *E. purpurascens*. Although he had observed and collected every species discussed in his monographic treatment, he had not observed live material from the southern Sierra Nevada, and thus did not recognize the significance of this solitary and disjunct collection.

The similarities between *E. pusaterii* and *E. grandiflorum* noted by Munz and Howell (large flowers, saclike appendages on the perianth, and unmottled leaves) are found in a number of western North American species, and do not characterize *E. pusaterii* and *E. grandiflorum* alone. *Erythronium pusaterii* is distinguished from *E. grandiflorum* by its bicolored, more numerous flowers (ranging up to 8 per scape); entire to short-lobed stigma; and shorter style, filaments, and anthers. *Erythronium grandiflorum* throughout its range has perianth segments that are golden yellow, lighter near the base (Applegate 1935), and anther color varying from cream to yellow or dark red. Various varieties and subspecies based on anther color



have been described; however, this criterion has proved to be of limited taxonomic value. Major floristic manuals within the range of this species do not recognize these infraspecific taxa (Cronquist et al. 1977; Hitchcock et al. 1969), and we concur with this interpretation.

*Rarity status.* *Erythronium pusaterii* has a highly restricted geographic range, occurring at only four locations in the upper Kaweah and Tule River watersheds. All populations are free from human disturbances at present. The South Fork Kaweah River populations are within Sequoia National Park where the species is adequately protected. Moses Mountain, the location of the largest numbers and concentrations of the Kaweah fawn lily, is within the Golden Trout Wilderness, Sequoia National Forest and is likewise protected. The populations within Sequoia National Forest on Jordan Peak and Slate Mountain are managed to conserve the species under Forest Service sensitive plant policy. The localized nature of the species distribution and level of field work conducted by the first author in the general area suggest that additional occurrences are unlikely to expand the range of this endemic species of the southern Sierra Nevada.

***Erythronium pluriflorum*** Shevock, Bartel and Allen, sp. nov. (Fig. 3)—TYPE: USA, California, Madera Co., Chiquito Ridge along the N and NE slope of Shuteye Peak on granitic rocky slopes, subalpine coniferous forest, Sierra National Forest, T7S, R23E, Sect. 2 N½, 8250 ft, 25 May 1989, *Shevock, Bartel, and Allen 11854* (holotype, CAS; isotypes, FSC, MO, NY, RSA, UC, US, UVIC).

Folia 7–40 cm longa elliptica vel oblanceolata non maculata; scapus floribus plerumque pluribus; flores tepalis 15–28 mm longis late lanceolatis recurvis luteis aetate subaeneis, sine appendiculis saccatis basalibus; antheris luteis, filamentis luteis tenuibus; stylo clavato luteo, stigmatе integro vel brevilobato, lobi minus quam 1 mm longis.

Bulb 5–7(–9) cm long, 1–2 cm wide. Leaves 2 (rarely 3), unmottled, bright green with undulate margins, 7–35(–40) cm long, 1.5–4.5(–6) cm wide, oblanceolate to elliptic. Scapes 7–35(–45) cm tall; flowers, 1–10(–21), nodding, pedicels of unequal lengths. Perianth segments recurved, elliptic to lanceolate, 15–28 mm long, 4–7 mm wide, bright yellow fading bronze to pinkish after anthesis, saclike basal appendages lacking. Filaments bright yellow, slender, the inner ones longer; anthers bright yellow, when dehiscent approximately ½ as long as the filaments; style bright yellow, clavate, stigma entire or with very short lobes (<1.0 mm). Pedicels elongating markedly after anthesis, erect, up to 12.5 cm long. Capsule obovoid, 25–35 mm



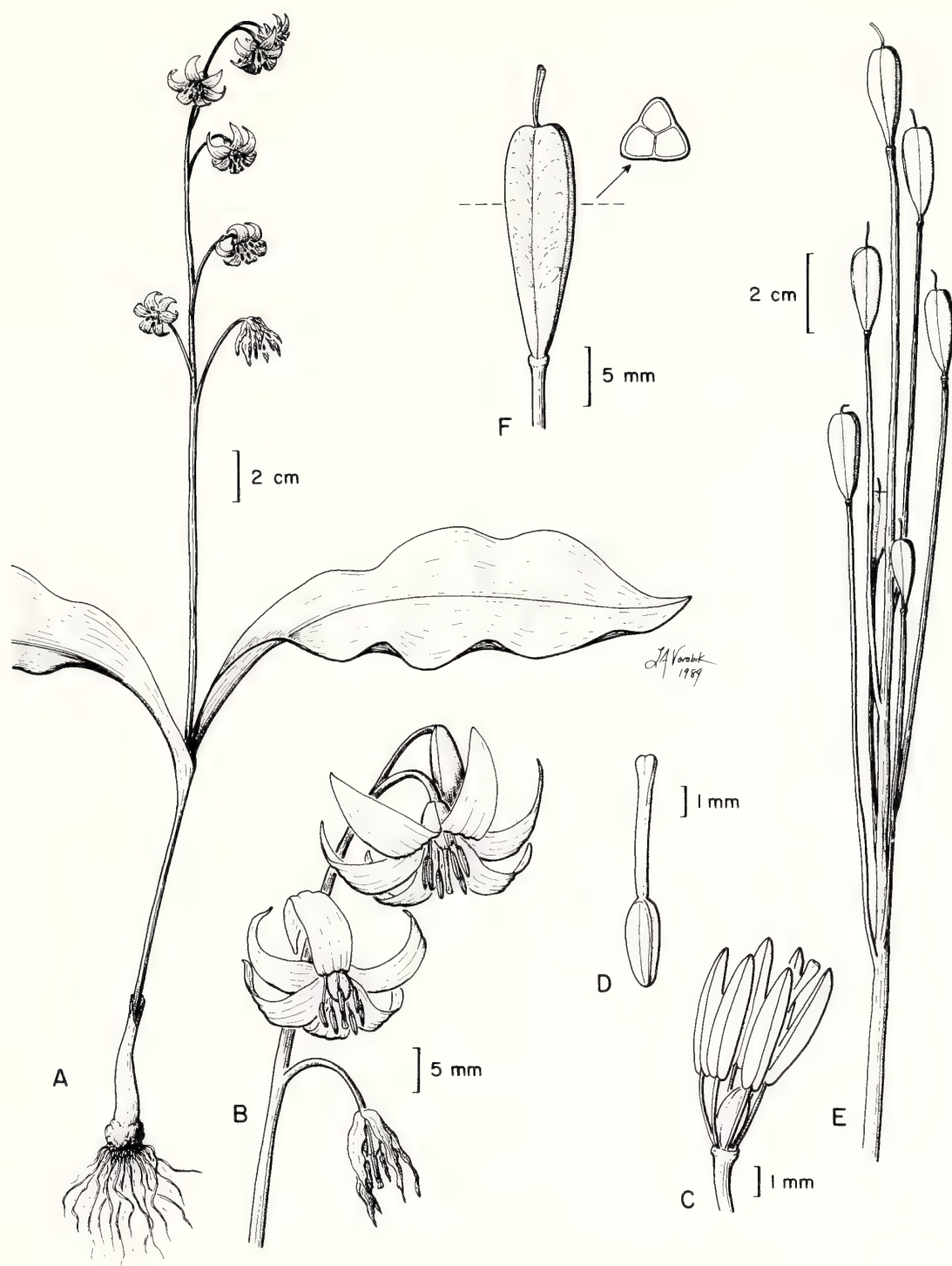


FIG. 3. *Erythronium pluriflorum*. A, habit; B, close-up of flowers; C, stamens; D, stigma; E, fruiting scape; F, capsule.

long, 6–10 mm wide. Seeds brown, narrowly elliptical in outline, flattened. Chromosome number:  $2n=24$ .

*Paratypes*. USA, California, Madera Co., type locality, 22 Aug 1907, *J. Murdoch Jr.* 554 (CAS [not located], GH!, NY!, US!) 23 Jun 1984, *MacFarlane s.n.* (CAS); 1 Jun 1988, *J. Clines* 148 (CAS), 29 Jun 1988, *Clines and Lorenzana* 158 (CAS, FSC); 2 Jul 1988, *Shevock and Bartel* 11844 (CAS, FSC, RSA, UC); Little Shuteye



Peak, T6S, R23E, Sect. 20 & 21, 7600–8300 ft, 13 Jun 1989, *Shevock 11857* (CAS, FSC, MO, NY, RM, RSA, UC, US, UVIC); road adjacent to Chilkoot Lake, T6S, R23E, Sect. 17 NW¼ NW¼, 7300 ft, 13 Jun 1989, *Shevock 11858* (CAS, RSA); rock outcrops ¼ mi S of Shuteye Pass, T7S, R23E, Sect. 12 NW¼, 7600 ft, 14 Jun 1989, *Shevock 11873* (CAS, FSC, MO, NY, RSA, UC, US, UVIC).

This distinctive, beautiful, many-flowered *Erythronium* was first brought to our attention by Joanna Clines, a seasonal employee hired by the Sierra National Forest in 1988 to do botanical surveys of rare species. A subsequent search of *Erythronium* collections at CAS, DAV, DS, FSC, JEPS, POM, RSA, and UC revealed one specimen collected by J. Murdoch Jr. in August 1907 that represents the first collection for this new species. This specimen was filed for 81 years among specimens of *E. purpurascens*. Both Applegate (1935) and Smiley (1921) cited the Murdoch collection as *E. purpurascens*. Roger MacFarlane, a Research Associate at CAS and student of Liliaceae, has recently studied selected members of *Erythronium*. He independently recognized that the Murdoch collection from “Shuteye Mountain” in Madera County did not represent *E. purpurascens*. Collections and photographs were obtained by MacFarlane on 23 June 1984. He correctly concluded that the Shuteye Peak plants were new to science (pers. comm.) but he did not formally describe the new species.

*Distribution, habitat and phenology.* *Erythronium pluriflorum* grows on rocky granitic slopes in a very open *Pinus monticola*–*Abies magnifica* forest from 2100–2700 m. Plants form large colonies in bedrock crevices and ledges where soil and humus accumulate. Flowering extends from mid-May to mid-July depending on snowpack duration and temperature. The Murdoch collection obtained in August 1907 represents the extreme range of flowering season, corresponding to an exceptionally heavy snowpack in the winter of 1906–1907 (Hill 1975:40). *Erythronium pluriflorum* is known from a few scattered populations along Chiquito Ridge from Chilkoot Lake and Little Shuteye Peak southward to Shuteye Peak and Shuteye Pass, San Joaquin River watershed, Sierra National Forest. Both the Shuteye Peak and Little Shuteye Peak populations number in the millions of individuals. Associated species include *Lomatium torreyi* (J. Coulter & Rose) J. Coulter & Rose, *Penstemon newberryi* A. Gray, *Saxifraga bryophora* A. Gray, *Sedum obtusatum* A. Gray subsp. *obtusatum*, *Sorbus californica* E. Greene, and *Triteleia dudleyi* Hoover.

*Relationships.* *Erythronium pluriflorum* most closely resembles *E. purpurascens* and *E. pusaterii*. All three species produce large numbers of flowers, commonly up to 8 per scape; which exceeds the 1–4 flowers per scape produced by the majority of *Erythronium* species. A unique feature for *E. pluriflorum* is the presence of two separate



phases of flower production on mature/robust individuals. Initially, each scape develops up to 8 flowers including the terminal flower for the raceme. The second flowering phase appears to be delayed until anthesis and pedicel elongation of the first phase. The second flowering phase is somewhat congested midway on the scape and the flowers are slightly smaller. These mature individuals can produce up to 21 flowers per scape. We are unaware of this flowering pattern occurring in any other species of *Erythronium*.

The single collection of *E. pluriflorum* known to Applegate (1935) and Smiley (1921) was placed within *E. purpurascens*, which is probably its nearest relative. Faded specimens of *E. purpurascens* and *E. pluriflorum* could be confused in herbaria, though they are easily distinguished in the field by tepal color. Other characteristics such as the larger leaves, and color of style and filaments also help to separate *E. pluriflorum* and *E. purpurascens*. The flowers of *E. pluriflorum* are bright yellow throughout and turn bronze to pinkish after anthesis while the flowers of *E. purpurascens* are white with a yellow base and become purple tinged with age. The leaves of *E. pluriflorum* and *E. pusaterii* are very similar in size, color, and appearance with undulate margins. Plant height is often similar as well. The species differ in flower size and color; those of *E. pusaterii* are nearly twice as large, with the terminal portions of the tepals white.

Both *E. pluriflorum* and *E. pusaterii* occur in soil pockets of high montane rocky summits. Although *E. purpurascens* occurs further north, its preferred habitat has similarities to those of these two species. Sites that appear to be suitable habitat for either *E. pluriflorum* or *E. pusaterii* occur within the 120 km that separate these two species (within Fresno County), but the deep canyons of the Kings and San Joaquin Rivers have probably served as major barriers for colonization of these habitats.

*Rarity status.* Although *Erythronium pluriflorum* is relatively abundant along Chiquito Ridge, this species is entirely limited to this locality comprising an area less than 0.5 km by 11 km. From a phytogeographical perspective, this is an extremely narrow montane endemic. Since this high elevation species has very specific growing conditions, the success in cultivation at low elevations is unlikely, and therefore it should not be collected for this purpose. None of the populations occur in any protected area; however, the Sierra National Forest will manage and conserve this species under Forest Service policy via their sensitive plant program.

*Conclusion.* We believe that all three endemic species of *Erythronium* in the Sierra Nevada are relictual taxa isolated from interaction with the remainder of the genus. Both *E. pluriflorum* and *E. pusaterii* are locally abundant, but extremely restricted in geographic range. Together with the more widespread *E. purpurascens*, they may be



relictual remnants of an ancestor that was once more widely distributed. The likelihood of extending the range for *E. tuolumnense*, *E. pluriflorum* and *E. pusaterii* appears to be remote. The extent of past glaciation in the Sierra Nevada is probably not so important to the distribution of *Erythronium* species as the subsequent shift to a warmer and drier climate, leading to a reduction and fragmentation of suitable habitat. The north-south orientation of the Sierra Nevada coupled with increasing elevational relief, narrowing width and increasing aridity as one proceeds southward may also aid in explaining the disjunct nature of *Erythronium* species in this mountain range. Most western North American *Erythronium* species are allopatric, and hybridization can occur in areas of sympatry (Applegate 1935; Allen and Antos 1988). However, natural hybridization between Sierran *Erythronium* species is lacking due to geographic isolation and other ecological/habitat parameters.

#### ACKNOWLEDGMENTS

We thank Joanna Clines for the *Erythronium* collection that provided the catalyst for this paper and John Lorenzana of the Sierra National Forest for assistance, photographs and field notes. The assistance of Roger MacFarlane, for making his data accessible to the authors is also greatly appreciated. We are grateful to the curators of GH, NY, and US for loan of specimens. Special thanks to Linda Vorobik from the Jepson Herbarium for providing the excellent botanical illustrations. We also thank Wayne Ferren, Rodney Myatt, and Dale McNeal for providing ways to make this paper more informative.

#### LITERATURE CITED

- ALLEN, G. A. and J. A. ANTOS. 1988. Morphological and ecological variation across a hybrid zone between *Erythronium oregonum* and *E. revolutum* (Liliaceae). *Madroño* 35:32–38.
- APPLEGATE, E. I. 1935. The genus *Erythronium*: a taxonomic and distributional study of the western North American species. *Madroño* 3:58–113.
- CAVE, M. 1970. Chromosomes of the California Liliaceae. *Univ. Calif. Publ. Bot.* 57:22–24.
- CRONQUIST, A., A. H. HOLMGREN, N. H. HOLMGREN, J. L. REVEAL, and P. K. HOLMGREN. 1977. Intermountain flora, vol. 6. Columbia Univ. Press, New York.
- HILL, M. 1975. Geology of the Sierra Nevada of California. U.C. Press, Berkeley.
- HITCHCOCK, C. L., A. CRONQUIST, M. OWNBEY, and J. W. THOMPSON. 1969. Vascular plants of the Pacific northwest. Vol. 1. Univ. Washington Press, Seattle.
- JEPSON, W. L. 1923. A manual of the flowering plants of California. U.C. Press, Berkeley.
- KARTESZ, J. T. and R. KARTESZ. 1980. A synonymized checklist of the vascular flora of the United States, Canada, and Greenland. Vol. 2. Univ. North Carolina Press, Chapel Hill.
- MUNZ, P. A. 1968. A supplement to a California flora. Univ. California Press, Berkeley.
- and J. T. HOWELL. 1964. The Kaweah fawn lily, a new subspecies in California. *Leaflet West. Bot.* 10:104–105.
- and D. D. KECK. 1959. A California flora. Univ. California Press, Berkeley.
- SHEVOCK, J. R. 1977. Sensitive plant species of Sequoia National Forest and adjacent regions. USDA—Forest Service, Porterville, CA. 187 pp.



- and D. W. TAYLOR. 1987. Plant exploration in California, the frontier is still here. Pp. 91–98 in T. S. Elias (ed.), *Conservation and management of rare and endangered plants*. California Native Plant Society, Sacramento, CA.
- SMILEY, F. 1921. A report on the boreal flora of the Sierra Nevada of California. *Univ. Calif. Publ. Bot.* 9:1–423.
- WILLIS, J. C. 1973. *A dictionary of flowering plants and ferns*, eighth ed. Cambridge Univ. Press.

(Received 30 Nov 1989; revision accepted 22 May 1990.)

## ANNOUNCEMENT

### AWARDS FOR BEST PAPERS: CALIFORNIA BOTANICAL SOCIETY THIRTEENTH GRADUATE STUDENT MEETINGS

#### *Completed Research* (\$100)

AARON LISTON, Department of Genetics, University of California, Davis—Evidence for rapid allopatric speciation in *Astragalus* section *Leptocarpi* subsection *Californici*

#### *Research in Progress* (\$100)

CLAUDIA M. TYLER, Department of Biological Sciences, University of California, Santa Barbara—Factors affecting seedling establishment in chaparral after fires.

#### *Proposed Research* (tie, \$50 each)

RANDY K. ZEBELL, Department of Biological Sciences, San Francisco State University, San Francisco—A biosystematic investigation of variation in *Calochortus venustus*

MAILE C. NEEL, Department of Biological Sciences, University of California, Santa Barbara—Morphological and allozyme variation in *Echinocereus engelmannii* var. *munzii*



CYTOLOGICAL, MORPHOLOGICAL, ECOLOGICAL AND  
PHENOLOGICAL SUPPORT FOR SPECIFIC STATUS OF  
*CRATAEGUS SUKSDORFII* (ROSACEAE)

STEVEN J. BRUNSFELD and FREDERIC D. JOHNSON  
Department of Forest Resources,  
College of Forestry, Wildlife and Range Sciences,  
University of Idaho

ABSTRACT

Field and herbarium studies have revealed the presence of 20-stamen black-fruited hawthorns (*Crataegus*) from 29 sites in the northern Rocky Mountains. This entity has often been treated as a variety of the 10-stamen species, *C. douglasii*, and was formerly believed to be essentially restricted to west of the Cascade/Sierra Range. We present evidence that the 20-stamen form is diploid whereas *C. douglasii* is tetraploid, and that the two differ substantially in morphology, ecology and phenology. These lines of evidence strongly support Kruschke's treatment of the 20-stamen entity as a distinct species, *C. suksdorfii*.

The black-fruited hawthorns, Sect. *Douglasii* Loud., constitute the most widespread and abundant members of *Crataegus* L. in western North America. The group consists of three entities that have been treated as distinct species (Kruschke 1965), or as varieties of one species, *Crataegus douglasii* Lindl. (e.g., Hitchcock et al. 1961; Scoggan 1978). *Crataegus suksdorfii* (Sarg.) Kruschke (*C. douglasii* var. *suksdorfii* Sarg.) is distinctive in having 20 stamens, and was previously thought to be distributed: "entirely west of the Cascades except inland somewhat in the Fraser R. Valley and Columbia R. Gorge" (Hitchcock et al. 1961); and confined to the "Coastal Douglas-Fir" zone in British Columbia (Taylor and MacBryde 1977). The second form, *C. douglasii* (var. *douglasii*), has 10 stamens and is widespread in the northern Rocky Mountain region, occurring occasionally west of the Cascades in the Puget Sound and the Columbia River Gorge, and also disjunct in northern Michigan and southwestern Ontario (Hitchcock et al. 1961). The third form, *C. rivularis* (var. *rivularis*), has 10 stamens, is distributed in the central Rocky Mountains, and differs from *C. douglasii* in its leaf shape and branching pattern. *Crataegus rivularis* is poorly understood and will not be considered further in this paper.

Differences in stamen number, especially 10 vs. 20 stamens, are found in many species groups in *Crataegus*. Some early workers (e.g., Eggleston 1908; Palmer 1946) considered this variation relatively trivial and did not use stamen number as an important basis for distinguishing species. Kruschke (1965), however, placed con-



siderable weight on this trait; he stated "a 10-stamen entity can not be a variety of a 20-stamen entity or conversely so". On this basis, and perhaps other unmentioned characters, he elevated many taxa, including *C. suksdorfii*, to specific status. Phipps and Muniyamma (1980) have noted that taxa differing in stamen number generally have other associated distinguishing features.

The recent discovery of 20-stamen hawthorns sympatric with 10-stamen forms in the northern Rocky Mountains has prompted a reevaluation of the taxonomy of these two entities. Our investigations provide evidence from cytology, morphology, ecology, and phenology that *C. suksdorfii* should indeed be considered a distinct species.

#### DISTRIBUTION

Since 1981, when a specimen of 20-stamen *Crataegus* from Idaho first came to our attention (*Wellner* 2258), we have gathered extensive field and herbarium data (ID, IDF, MONTU, MRC, ORE, WS, UW) on the black-fruited hawthorns of the northern Rocky Mountain region. Figure 1 illustrates the formerly-known western distribution of *C. suksdorfii*, and the locations of 29 newly-confirmed northern Rocky Mountain populations (representative specimens are given in Table 1). The disjunct range extends from about latitude 49° to 53°N, a distance of about 1000 km. Inland Rocky Mountain and coastal populations are disjunct 200–400 km from one another throughout most of their range, but the gap is somewhat bridged by populations in the Fraser R. drainage in interior British Columbia, and three isolated collections from east of the Cascade crest in central Washington and Oregon (Fig. 1). The two Washington sites are from the east slope of Cascades, east of the formerly-described range, but following a pattern seen in many other "west side" species such as *Cornus nuttallii* and *Acer circinatum* (Hitchcock et al. 1961). The third outlier, in central Oregon, appears to be a continuation of the Columbia River Gorge eastward extension of range. The type locality of *C. suksdorfii*, indicated by an open circle in Figure 1, is at the east end of the Columbia River Gorge in Klickitat Co., Washington. Figure 1 also shows the principal range of *C. douglasii*, which is partially sympatric with the disjunct inland *C. suksdorfii* element reported here. Herbarium data also confirm that there is localized sympatry in the Puget Sound/Vancouver Island region and the Columbia River Gorge. We have not examined the extent of sympatry or the ecological relationships between the species at these western points of contact.

#### EVIDENCE FOR SPECIFIC STATUS OF *CRATAEGUS SUKSDORFII*

Species concepts in *Crataegus* have been notoriously variable. For example, estimates by various workers for the number of *Crataegus*



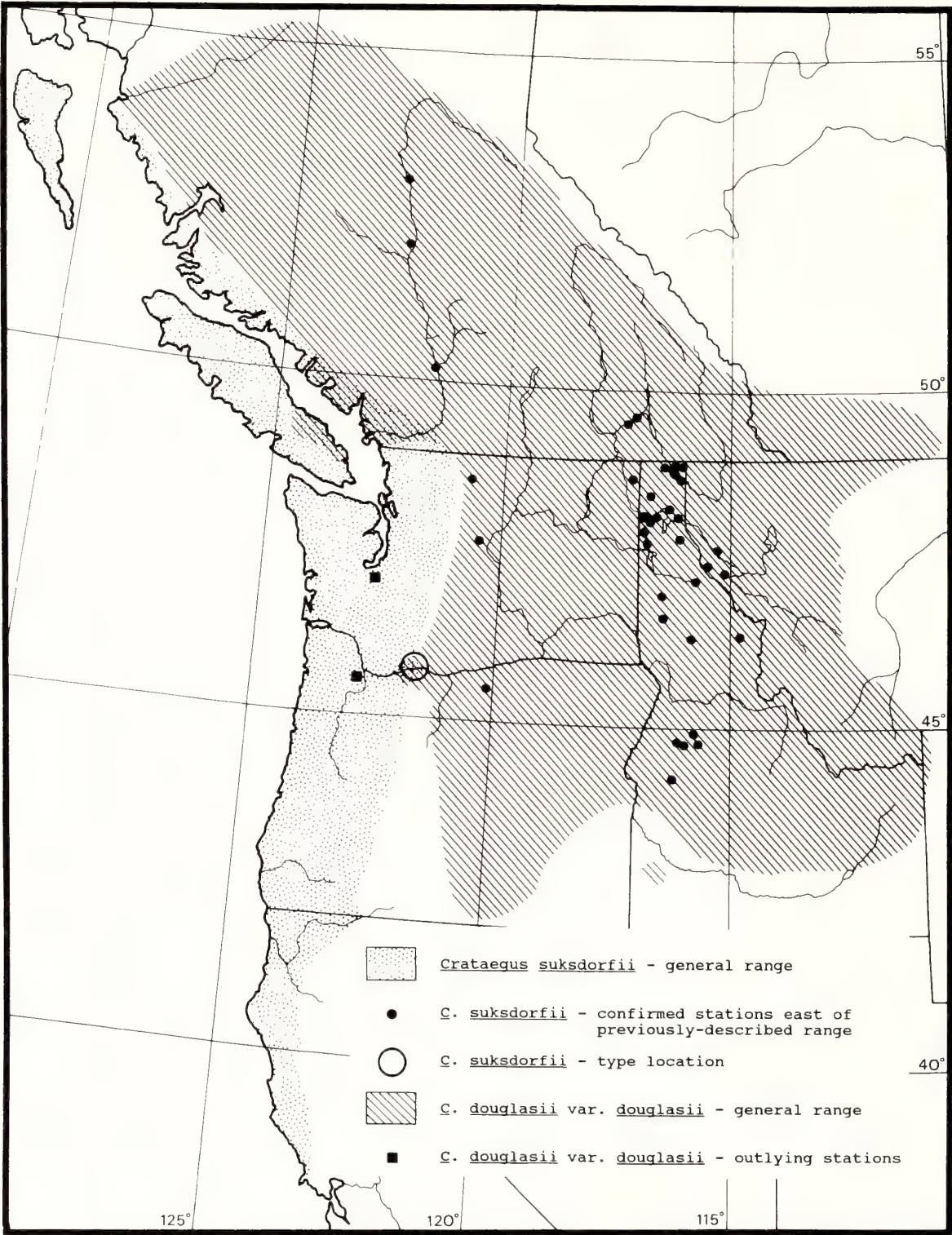


Fig. 1. Ranges of *Crataegus suksdorfii* and *C. douglasii* (var. *douglasii*). Generalized ranges based on Little (1976), herbarium data and floras cited in text.

species in Ontario range from 8 to 91 (Phipps and Muniyamma 1980). Until recent years species concepts were based largely on the principal data at hand: morphology seen on herbarium sheets. In modern biosystematic studies decisions on what constitutes a species are generally based on assessments of the reproductive biology and the overall genetic divergence of the populations under consider-



TABLE 1. REPRESENTATIVE SPECIMENS OF *CRATAEGUS SUKSDORFII* FROM THE INTERIOR/ROCKY MOUNTAIN REGION.

---

Canada, British Columbia, Willow Point, Kootenay Lake, 49°33'N, 117°15'W, *Eastham* 9022 (UBC); Quesnel Dam, 52°58'N, 122°30'W, *Newcombe* 377 (UBC). United States, Idaho: Boundary Co., Smith Lake, *Johnson and Brunsfeld* 1954 (ID, IDF); Hideaway Island, Kootenai R., *Wellner* 2258 (ID); Bonner Co., Priest River Exp. Forest, *Daubenmire* 44264 (WS); Kootenai Co., E fork of Hayden Ck, vic. Hayden Lake, *Johnson* 86134 (ID, IDF); Shoshone Co., Coeur d'Alene R. vic. Spion Kop Ck., *F. D. Johnson and C. L. Johnson* 1574 (ID, IDF); Benewah Co., St. Maries R. vic. Soldier Ck., *Brunsfeld and Johnson* 2802 (ID, IDF); Idaho Co., Lochsa R. at Wendover Ck., *Johnson and Brunsfeld* 2800 (ID, IDF); Valley Co., Middle Fork Payette R. vic. Trail Ck. Campground, *Kramer* N192 (IDF). Montana: Missoula Co., Miller Ck., *Hitchcock* 1762 (MONTU); Mineral Co., 0.5 mi E of Lookout Pass, *Johnson and Smith* s.n. (IDF)., Washington: Pend Oreille Co., Sullivan Lake, *Johnson* 8931 (ID, IDF); 6 mi N of Newport, *Jones* 5645 (WTU).

---

ation. If a group of populations is reproductively isolated and possesses significant genetic distinctions, as manifested by morphology, ecology, phenology, molecular measures, etc., the criteria of both the biological species concept and the taxonomic species concept are satisfied (Grant 1981). We present four lines of evidence that together strongly support the treatment of *C. suksdorfii* as a biological and taxonomic species.

1) *Cytology*. Polyploidy is a common phenomenon in plants, and it generally results in speciation because ploidal differences effectively end most gene exchange (Grant 1981). The 10- and 20-stamen hawthorns considered here exist at different ploidal levels, and thus likely have a high degree of reproductive isolation. *Crataegus suksdorfii* is diploid ( $2n=34$ ) in its distribution west of the Cascade Range (Calder et al. 1968: Queen Charlotte Islands, B.C.,  $2n=34$ ). *Crataegus douglasii* has been reported to be tetraploid ( $2n=68$ ). The tetraploid count, however, was from a plant of unknown origin cultivated in Leningrad, USSR (Gladkova 1968). The chromosome number of *Crataegus douglasii* is listed as  $2n=51$  in the Flora of Alberta (Moss 1983), but no additional information is given.

We sought to confirm differences in ploidy level of 10- and 20-stamen populations from the sympatric Rocky Mountain region. Flower buds were fixed using standard techniques (Soltis 1980), and mitotic figures were obtained from preparations of tissue from young, meristematic petals (Dickinson and Phipps 1986). No pretreatment of the buds was performed. Counts were obtained from a site where both the 10- and 20-stamen entities occur: USA, Idaho, Adams Co., Goose Ck. near Last Chance Campground, *Cronk* 205—*Crataegus suksdorfii*,  $2n=34$  (ID, IDF); *Cronk* 192—*Crataegus douglasii*,  $2n=68$  (ID, IDF). An additional count of *C. douglasii* was obtained from



TABLE 2. CONSPECTUS OF MORPHOLOGICAL CHARACTERS OF *CRATAEGUS DOUGLASII* (VAR. *DOUGLASII*) AND *C. SUKSDORFII*.

| Character                           | <i>C. douglasii</i>                                   | <i>C. suksdorfii</i>                               |
|-------------------------------------|---|--|
| Flower width, dried (mm)            | 14–16   | 12–13  |
| Stamen number                       | 10  | 20   |
| Mature fruit, fresh diameter (mm)   | 9–10  | 7–8  |
| Pyrene length (mm)                  | 5.0   | 4.5  |
| Pyrene shape                        | dorsally rounded, plump, shallowly sculpted laterally | dorsally keeled, narrow, deeply sculpted laterally |
| Leaf shape on short shoots          | obovate, lobed above middle, truncate apex            | elliptic to obovate, unlobed, rounded apex         |
| Thorn length on older branches (mm) | 13–18   | 8–12   |

a population about 280 km to the north: USA, Washington, Whitman Co., vic. Pullman-Moscow Airport, *Brunsfeld 3012*,  $2n=68$  (IDF). Photomicrographs and camera-lucida drawings are on file with the authors. We conclude from this evidence that *C. suksdorfii* and *C. douglasii* are diploid and tetraploid, respectively. However, the possible triploid count for *C. douglasii* reported from Alberta may indicate that hybridization, or apomixis and fertilization of unreduced gametes occurs in this species as it does in some other polyploid hawthorns (Dickinson and Phipps 1986; Campbell and Dickinson 1990).

2) *Morphology*. Based on our field and herbarium observations, especially on Rocky Mountain populations, *Crataegus suksdorfii* differs substantially from *C. douglasii* in its floral and vegetative morphology (Table 2, Fig. 2). Because the species differ in flower, fruit, leaf and thorn, they can be distinguished with some certainty throughout the year. Thus they appear to be more clearly differentiated than a number of other recognized species pairs in *Crataegus* (Phipps and Muniyamma 1980).

3) *Ecology*. The discovery of numerous sympatric populations of these two entities allows a comparison of their ecological amplitudes. It has been observed that polyploid species often occupy a wider range of habitats than their diploid relatives (Stebbins 1971; Lewis 1980; Levin 1983). Thus polyploids are often able to tolerate temperature, moisture or soil conditions unsuitable to the diploid. This is clearly the case in this species pair.

In the northern Rockies, *C. suksdorfii* is almost exclusively found in cool, moist stream- and lakeside habitats within forest communities ranging from mid-montane (*Abies grandis*, *Thuja plicata*, and





Fig. 2. *Crataegus suksdorfii* (left) and *Crataegus douglasii* (right) from same locality: Idaho, Adams Co., Goose Cr. at junction with State Hwy. 55, F.D. Johnson 88068 and 88069 (IDF), both collected 10 August 1988.

*Tsuga heterophylla*) to the lower subalpine (*Abies lasiocarpa*) zones. The geographic distribution of *C. suksdorfii* (Fig. 1) conforms to the extent of maritime (coastal) climates in the Rocky Mountains, as manifested by the distribution of *Abies grandis*.

*Crataegus douglasii* has a substantially broader ecological amplitude in both temperature and moisture regimes. Habitats in the sympatric region range from low-elevation grassland and sagebrush zones, through the montane and lower subalpine forest zones. It inhabits streamside and bottomland sites, but also is common in seasonally drier, mesic, forested and nonforested upland habitats. For example, Cooper et al. (1987) present data for its occurrence beneath near climax upland stands of *Pinus ponderosa*, *Pseudotsuga menziesii* var. *glauca*, *Abies grandis*, and *Thuja plicata*. Daubenmire (1970) describes communities dominated by *Crataegus douglasii* in both riparian and upland habitats of the steppe region of Washington.

*Crataegus douglasii* is so ubiquitous in the Rocky Mountains, it not surprising that it was found in close proximity to many *C.*



*suksdorfii* populations. At these sites the species tend to be segregated: *C. suksdorfii* at lake or streamside, *C. douglasii* in adjacent meadows and uplands.

4) *Phenology and reproductive biology.* Where we have observed the species occurring together, *C. douglasii* begins flowering one to two weeks before *C. suksdorfii*, though there is some overlap in flowering times. Other workers have also documented differing phenologies for different *Crataegus* species at a site (e.g., Phipps and Muniyamma 1980; Dickinson and Phipps 1986). Fruiting phenology is reversed, with ripe, black fruits present on *C. suksdorfii*, while at the same time and site the fruits of *C. douglasii* are still largely immature. Apparently the larger fruits of tetraploid *C. douglasii* take several weeks longer to develop. Such developmental differences have been observed in other diploid/tetraploid species pairs (Levin 1983).

Despite the large number of populations in the newly-reported range, several lines of evidence suggest a limited reproductive potential for *C. suksdorfii* in this region. Most of the 29 populations reported here contain relatively few individuals and are of restricted geographic extent. This may reflect limited suitable habitat at many sites, but may also be the result of low seed output. We observed a high rate of seed abortion in *C. suksdorfii*, something also noted by Sargent (1907). In many populations we found that frequently at least 3 of the 5 pyrenes per fruit were unfilled. *Crataegus suksdorfii* has been reported to be self-incompatible (Love and Feigan 1978), which combined with small, isolated populations could affect fecundity. We did not observe a notable incidence of seed abortion in *C. douglasii*. Although many of the *C. suksdorfii* populations reported here are in close proximity to larger *C. douglasii* populations, *C. suksdorfii* appears to be largely maintaining its identity, probably due to intersterility conferred by ploidal differences and phenological and habitat separation. However, at several locations plants were collected that appear to be intermediate or atypical in thorn length and/or leaf characteristics. Additional study of the reproductive biology of these species is needed, particularly to assess the role of apomixis in *C. douglasii*.

## DISCUSSION

The discovery of widespread populations of *C. suksdorfii* in the Rocky Mountains is not only of phytogeographical interest, but also provides insights into the relationship between *C. suksdorfii* and its sister taxon *C. douglasii*. Although it is remarkable that such a widespread and conspicuous species could go undetected until now, the presence of another Pacific coastal species in the northern Rocky Mountain flora is no surprise. Montane vegetation of the western



portion of the northern Rocky Mountains is basically a disjunct extension of a coastal ecosystem that was fragmented by the climatic changes created by the uplift of the Cascade Range in the Pliocene. *Crataegus suksdorfii* joins a long list of plant and animal species whose principal distribution is west of the Cascades, but which also occur in the region of maritime climate in the northern Rocky Mountains (Lorain 1988).

The sympatry between *C. suksdorfii* and *C. douglasii* in the northern Rocky Mountains provides us with an opportunity to make more profound judgments of their biological relationships. We now believe that these entities are reproductively isolated by virtue of their ploidal differences likely supplemented by phenological and ecological separation. They can be easily distinguished by a suite of floral and vegetative traits, which in concert with phenological and ecological differences indicate significant genetic divergence. These entities would appear to qualify as segregate species by the criteria of both the biological and taxonomic species concepts.

#### ACKNOWLEDGMENTS

We thank Tom Wells for his careful examination of UBC specimens and for assistance with cytology; Tim Dickinson for his advice throughout the project, and helpful suggestions on the manuscript; and the Directors of MONTU, MRC, ORE, WS, and UW for allowing us to examine their specimens. This research was supported by the C. R. Stillinger Foundation and the Forest, Wildlife and Range Experiment Station, University of Idaho. This is paper #519 of that station.

#### LITERATURE CITED

- CALDER, J. A., R. L. TAYLOR, and G. A. MULLIGAN. 1968. Flora of the Queen Charlotte Islands. Canad. Dept. of Agriculture Monograph 4. Vol. II.
- CAMPBELL, C. S. and T. A. DICKINSON. 1990. Apomixis, patterns of morphological variation, and species concepts in subfam. Maloideae (Rosaceae). Syst. Bot. 15: 124–135.
- COOPER, S. V., K. E. NEIMAN, R. STEELE, and D. W. ROBERTS. 1987. Forest habitat types of northern Idaho: second approximation. USDA-FS, Intermt. Res. Sta. Gen. Tech. Rept. INT-236, Ogden, UT.
- DAUBENMIRE, R. F. 1970. Steppe vegetation of Washington. Wash. Ag. Exp. Sta. Tech. Bull. G2, Pullman, WA.
- DICKINSON, T. A. and J. B. PHIPPS. 1986. Studies in *Crataegus* (Rosaceae: Maloideae) XIV. The breeding system of *Crataegus crus-galli sensu lato* in Ontario. Amer. J. Bot. 73:116–130.
- EGGLESTON, W. W. 1908. The Crataegi of the northeastern United States and adjacent Canada. Rhodora 10:73–84.
- GLADKOVA, V. N. 1968. Karyological studies on the genera *Crataegus* and *Cotoneaster* (Maloideae) as related to their taxonomy. Bot. Zhurn. 53:1263–1273.
- GRANT, V. 1981. Plant speciation. Columbia Univ. Press, NY.
- HITCHCOCK, C. L., A. CRONQUIST, M. OWNBEY, and J. W. THOMPSON. 1961. Vascular plants of the Pacific Northwest, Vol. 3. Univ. of Wash. Press, Seattle, WA.
- KRUSCHKE, E. P. 1965. Contributions to the taxonomy of *Crataegus*. Milwaukee Public Mus. Publ. Bot. No. 3.
- LEVIN, D. A. 1983. Polyploidy and novelty in flowering plants. Amer. Nat. 122: 1–25.



- LEWIS, W. H. 1980. Polyploidy in species populations. Pp 103–144 in W. H. Lewis (ed.), Polyploidy-biological relevance. Plenum Press, NY.
- LITTLE, E. L. 1976. Atlas of United States trees. Vol. 3. Minor western hardwoods. Misc. Publ. No. 1314, U.S. Dept. of Ag., Forest Service, Wash., D.C.
- LORAIN, C. C. 1988. Floristic history and distribution of coastal disjunct plants of the northern Rocky Mountains. M.S. Thesis, Univ. of Idaho, Moscow, ID.
- LOVE, R. and M. FEIGEN. 1978. Interspecific hybridization between native and naturalized *Crataegus* (Rosaceae) in western Oregon. *Madroño* 25:211–217.
- MOSS, E. H. 1983. Flora of Alberta, 2nd ed., rev. J. G. Packer. Univ. Toronto Press, Toronto, ON.
- PALMER, E. J. 1946. *Crataegus* in the northeastern and central U.S. and adjacent Canada. *Brittonia* 5:471–490.
- PHIPPS, J. B. and M. MUNIYAMMA. 1980. A taxonomic revision of *Crataegus* (Rosaceae) in Ontario. *Canad. J. Bot.* 58: 1621–1699.
- SARGENT, C. S. 1907. The black-fruited *Crataegus* of western North America. *Bot. Gaz. (Crawfordsville)* 44:64–66.
- SCOGGAN, H. J. 1978. The flora of Canada. Nat. Mus. Nat. Sci., Nat. Mus. Canada, Ottawa.
- SOLTIS, D. E. 1980. Karyotypic relationships among species of *Boykinia*, *Heuchera*, *Mitella*, *Sullivantia*, *Tiarella*, and *Tolmiea* (Saxifragaceae). *Syst. Bot.* 5:17–29.
- STEBBINS, G. L. 1971. Chromosomal evolution in higher plants. Addison-Wesley, Reading, Mass.
- TAYLOR, R. L. and B. MACBRYDE. 1977. Vascular plants of British Columbia: a descriptive resource inventory. Univ. of British Columbia, Vancouver, BC.

(Received 20 Feb 1990; revision accepted 6 Aug 1990.)

## ANNOUNCEMENT

### NEW MADROÑO EDITOR

The Executive Council of the California Botanical Society is pleased to announce the appointment of Dr. Jon E. Keeley to the position of Editor of *Madroño*. Dr. Keeley is professor of Biology at Occidental College. His editorship will commence in January 1991 with volume 38. All new manuscripts submitted to *Madroño* and all returned revisions should be mailed to him at the Department of Biology, Occidental College, Los Angeles, CA 90041. Dr. David J. Keil, who has completed his term as Editor, will be appointed to the Board of Editors to assist with continuity of journal management.



**BERBERIS PIMANA (BERBERIDACEAE): A NEW  
SPECIES FROM NORTHWESTERN MEXICO**

**JOSEPH E. LAFERRIÈRE**

Department of Ecology and Evolutionary Biology,  
University of Arizona, Tucson, AZ 85721

**JORGE S. MARROQUÍN**

Facultad de Ciencias Forestales,  
Universidad Autónoma de Nuevo León, Unidad Linares,  
Apartado Postal #41, 67700 Linares, N.L., México

**ABSTRACT**

**Berberis pimana** is described as a new species from the Sierra Madre Occidental, Chihuahua, Mexico. The species appears related to members of Sect. *Horridae* but is distinguished from other members of this section by its yellow to reddish seeds, shorter and thinner spines, and lack of hypodermal leaf layer. A new combination, **Berberis muelleri**, is published for the species previously known as *Mahonia muelleri*.

**RESUMEN**

**Berberis pimana** se describe como nueva especie de la Sierra Madre Occidental, Chihuahua, México. La especie parece emparentada con miembros de la Sección *Horridae* pero se distingue de las especies de esta sección por sus semillas amarillas o rojas, sus espinas más cortas y más delgadas, y por su ausencia de estrato hipodérmico en la hoja. Una nueva combinación, **Berberis muelleri**, se propone para la especie anteriormente conocido como *Mahonia muelleri*.

During ethnobotanical investigations among the Mountain Pima of the Sierra Madre Occidental of Chihuahua, Mexico, Laferrière collected specimens of *Berberis* which could not be assigned to any known species. We therefore describe the following new taxon.

**Berberis pimana** Laferrière & Marroquín, sp. nov. (Fig. 1)—TYPE: MEXICO, Chihuahua, Mpio. Temósachi, Nabogame, 1800 m, 28°30'N, 108°30'W, 19 Aug 1988, *Laferrière 1693* (holotype, ARIZ; isotypes, ANSM, CHAP, ENCB, MEXU, US).

Frutex 1–3 m altus. Caules fasciculati. Folia imparipinnata, rachidi articulata et petiolo persistenti; foliola 5–9(–13), articulata, sessilia, glabra, coriacea sed sine hypodermate, lanceolata, acuminata, mucronata, inferne glaucescentia, jugo inferno 4–7 mm supra basem; venatio reticulata, nervo medio conspicuo; dentes 4–7 per marginem, 0.1–1.5 mm longi, omnes cum spina 0.3–1.7 mm longa et 0.15–0.20 mm diametro. Racemi solitari vel 2–4 fasciculati, 3–8 cm longi, laxi, floribus 5–7, corymbosi; prophylla 2, 1–2 mm longa,



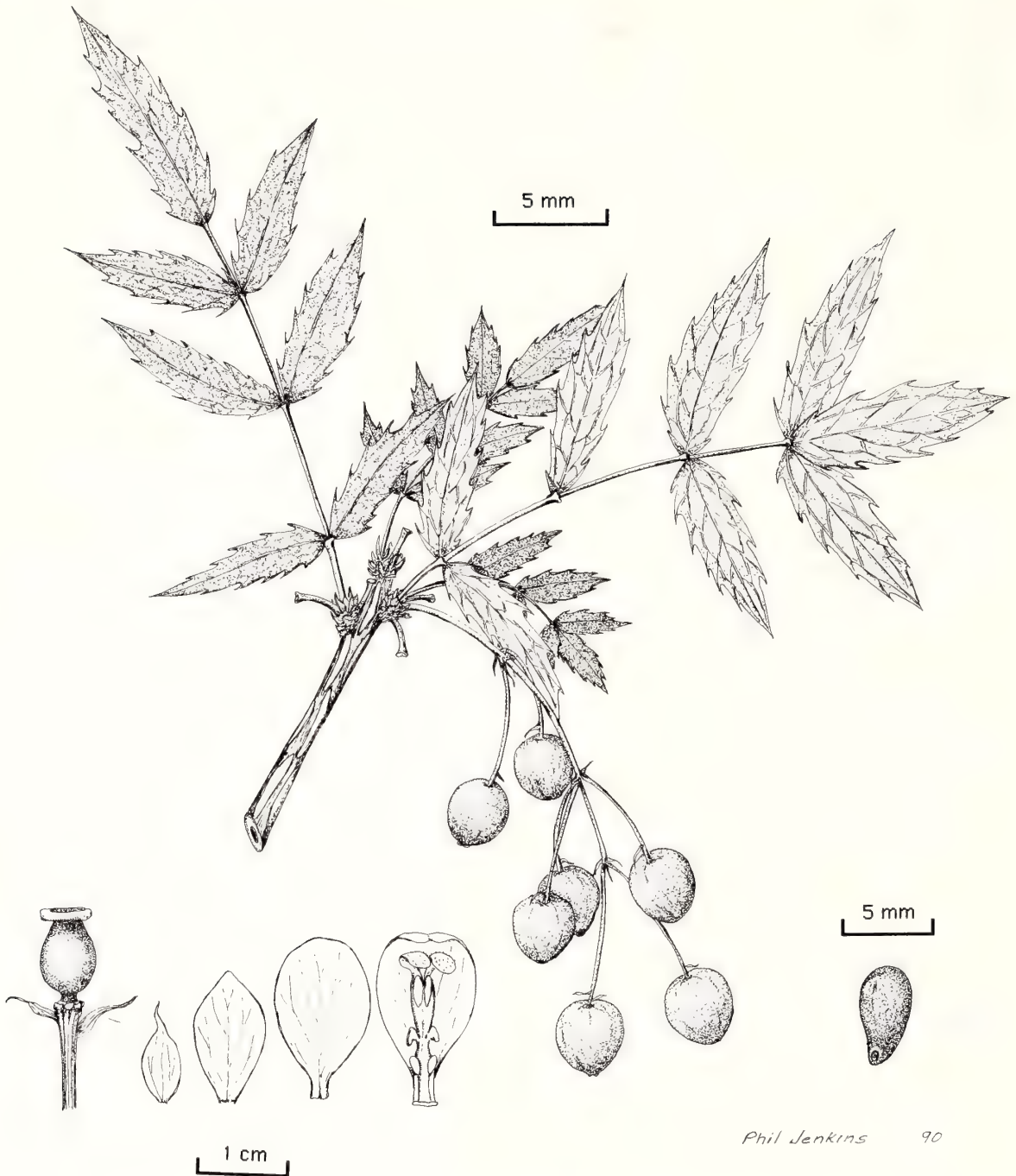


FIG. 1. Drawings of *B. pimana* (Laferrrière 359, 1694). Above, fruiting specimen, upper leaf surface at left, lower surface at right. Lower right, flower parts; Lower right, seed. Drawings courtesy Phil Jenkins.

persistencia, 0–8 mm infra perinathium affixa. Filamenta lata, dentata. Ovaria ovoidea, stigmatibus sessilibus, discoideo, atro, in fructu capitato ad sphaerico. Baccae coccineae, subglobosae ad ovoideae, pruinosae. Semina flavida ad succinea vel rubra, clavata ad ellipsoidea.

Shrub 1–3 m tall. Stems clumped, gray, rugose; wood yellow. Leaves 4–13 cm long, imparipinnate, with articulate rachis and persistent petiole; leaflets 5–9(–13), articulate to rachis, sessile, glabrous, coriaceous but lacking a hypodermis, 0.2 mm thick, lanceolate, mu-



cronate and slightly acuminate at the tip, obtuse and somewhat unequal or slightly rounded at the base, glaucescent below, with reticulate venation and a conspicuous costa, the margins each with 4–7 teeth 0.1–1.5 mm long, each bearing a terminal spine 0.3–1.7 mm long and 0.15–0.20 mm in diam; lateral leaflets 1–3 cm long, 4–12 mm broad, the lowermost pair 4–9 mm above base; terminal leaflet 1–5 cm long, sessile or petiolulate. Racemes axillary, single or in fascicles of 2–4, semi-erect at anthesis but pendulous at maturity, 3–8 cm long, loosely 5–7-flowered, corymbose, the peduncle firm, flattened, 0.8 mm wide, 0.2–0.3 mm thick; basal bracts 1.5–3 mm long, coriaceous, persistent; pedicels alternate or opposite, 10–15 mm long, 0.1–0.2 mm thick, flattened; prophylls 2, 1–2 mm long, persistent, attached 0–8 mm below the perianth. Flowers small; outer 3 sepals lanceolate, 2–4 mm long, green to yellow; inner 6 sepals obovate, 5–7 mm long, yellow; petals 6, obovate, 6–8 mm long, yellow, each opposite a single stamen; filaments thick, dentate; anthers white; ovary ovoid; stigma sessile, discoid, black, in fruit capitate to spherical. Berries 4–8 mm long, 6–10 mm broad, scarlet, subglobose to ovoid, pruinose, acidic but edible. Seeds 3–10, 3.5–4.5 mm long, 1.5–2.4 mm wide, clavate to ellipsoid, pale yellow to amber or reddish.

*Paratypes.* MEXICO. Chihuahua. Nabogame, 23 Apr 1987, in flower, *Laferrière* 359 (ANSM, ARIZ, K, MEXU, MO); 11 Jul 1988, in flower, *Laferrière* 1506 (ARIZ, CAN, CHAP, ENCB, MEXU); 18 Oct 1988, *Laferrière* 2109 (ARIZ, COLO, ENCB, TEX); *Acer grandidentatum* grove near banks of Río Yepachi, 5 km S of Nabogame, 6 Jul 1988, *Laferrière* 1490 (ARIZ); same locality, 19 Aug 1988, *Laferrière* 1694 (ARIZ, UNM); Las Varitas, 14 km W of Yepachi, 17 Jul 1988, *Laferrière* 1516 (ARIZ, MEXU, UC); Chihuahua, 29 Aug 1936, *LeSueur* 1186 (ARIZ). Sonora: 19.5 km W of Yécora, canyon with perennial stream and *Cupressus arizonica*, 1500 m, shrub to 3 m, uncommon, 4 Jun 1976, *D. E. Goldberg* 76-157 (ARIZ, ENCB).

The plant is named “pimana” in honor of the Mountain Pima inhabitants of the region in which the plant is found. The berries of this plant are eaten by some of the Pima inhabitants of the area but are considered too sour by others.

Figure 2 shows the locations of the known sites. *Berberis pimana* is found in shaded habitats near streams, usually under *Cupressus arizonica* E. Greene or *Acer grandidentatum* Nutt., but it also occasionally occurs on the northern (shaded) side of large boulders.

#### TAXONOMIC RELATIONSHIPS

The compound leaves of *B. pimana* place it in the group often segregated as the genus *Mahonia*. We prefer to treat this group as





FIG. 2. Map showing location of known collection sites of *B. pimana* in Chihuahua and Sonora, Mexico. Circle indicates type locality.

part of *Berberis* rather than as a separate genus. Moran (1982) suggested that *Berberis* sensu stricto may be a polyphyletic taxon. Whether this is true or not, *Mahonia* is very likely a paraphyletic grouping ancestral to the simple-leaved *Berberis*, because compound leaves are an ancestral character of the family (Loconte and Estes 1989; Ernst 1964). In either case, it seems preferable to treat the group as a single genus and deal with taxonomic relationships at the



subgeneric and sectional levels. The following new combination is required for the subsequent discussion:

***Berberis muelleri*** (I. M. Johnston) Marroquín ex Laferrière & Marroquín, comb. nov.—*Mahonia muelleri* I. M. Johnston, J. Arn. Arbor. 31:189–190, 1950.

This species was discussed by Marroquín (1972) but the combination was not formally published. The plant is native to the Sierra Madre Oriental of Nuevo Leon. This plant is similar to *B. pimana* but is distinguished by elliptic to ovate leaflets, inflorescence 15–20 mm long, and bracts 6 mm long.

Several characters suggest a relationship between *B. pimana* and Sect. *Horridae* Fedde (1901): short, few-flowered inflorescences; thin peduncles; ovoid, pruinose, many-seeded fruit; and clumped, shrubby growth habit. The only other compound-leaved species of the genus known to possess red fruits are all members of Sect. *Horridae*: *B. haematocarpa* Wooton, *B. nevinii* A. Gray, *B. higginsae* Munz, *B. trifoliolata* Moric., *B. pinifolia* (Lindl.) C. H. Mull., and *B. swaseyi* Buckley (Ahrendt 1961; Correll and Johnston 1970). Red fruits are also reported in several simple-leaved Asiatic species (Ahrendt 1961). Two other members of this section, *B. fremontii* Torrey and *B. muelleri*, also resemble *B. pimana* in the very long upwardly-spreading branches that lack further distal branching. Furthermore, they are also similar in the general gray color of the leaves whose pairs of leaflets are remote along the rachis.

*Berberis pimana* is unusual among the compound-leaved members of the genus in its yellow to reddish seeds. Most of the other members of the genus possess purple to dark brown seeds, except for a few simple-leaved species native to East Asia (Ahrendt 1961). In addition to the yellow seeds, *B. pimana* is distinguished from other members of Sect. *Horridae* by shorter, thinner spines and lack of a hypodermal layer in the leaves. This translucent layer, up to 0.01 mm thick, is present along the upper surface in all other members of the section, and results in the thick, stiff leaves and inconspicuous venation characteristic of the section. The hypoderm extends into the teeth and spines as well, increasing them to approximately 0.3 mm in diameter. The thinner leaves of *B. pimana* are likely correlated with its more mesic habitat. Most of the other members of Sect. *Horridae* are located in warmer, more arid regions.

#### ACKNOWLEDGMENTS

This work was supported in part by an NSF doctoral dissertation grant to the senior author and Dr. Willard Van Asdall. We also thank the curators of ANSM, ARIZ, ENCB, and MEXU for use of facilities and loan of specimens, and Charles Mason,



Reid Moran, Steve McLaughlin, Henry Loconte, Wayne R. Ferren, Jr., and James Henrickson for helpful critiques of the manuscript, and Phil Jenkins for assistance with illustrations.

#### LITERATURE CITED

- AHRENDT, L. W. A. 1961. *Berberis* and *Mahonia*: a taxonomic revision. J. Linn. Soc. Bot. 57:1–410.
- CORRELL, D. S. and M. C. JOHNSTON. 1970. Manual of the vascular plants of Texas. Texas Research Foundation, Renner, Texas.
- ERNST, W. R. 1964. The genera of Berberidaceae, Lardizabalaceae, and Menispermaceae in the southeastern United States. J. Arn. Arbor. 45:1–35.
- FEDDE, F. 1901. Versuch einer Monographie der Gattung *Mahonia*. Bot. Jahrb. 31: 30–133.
- LOCONTE, H. and J. R. ESTES. 1989. Phylogenetic systematics of Berberidaceae and Ranunculales (Magnoliidae). Syst. Bot. 14:565–579.
- MARROQUÍN, J. S. 1972. A monographic study of the genus *Berberis* L. in Mexico. Doctoral dissertation, Northeastern University, Boston.
- MORAN, R. 1982. *Berberis claireae*, a new species from Baja California; and why not *Mahonia*. Phytologia 52:221–226.

(Received 27 Apr 1989; revision accepted 22 May 1990.)

## ANNOUNCEMENT

### INTERNATIONAL CONFERENCE ON SERPENTINE ECOLOGY

International Conference on Serpentine Ecology, June 19 to 23, 1991, at University of California, Davis. The conference will focus on the contributions of those scientists who have done significant work on the ecology of serpentine soils. Small in size, the conference intends to bring together in an intimate setting the more senior as well as young investigators of the “serpentine syndrome”. The program will consist of contributed and invited papers, plus field trips. We invite any who have made contributions in edaphic and metallophyte ecology, particularly on serpentine systems, to make inquiries to:

Dr. A. R. Kruckeberg  
Dept. of Botany  
Univ. of Washington  
Seattle, WA 98195

Dr. Lin Wu (local organizer)  
Dept. of Environmental Hort.  
Univ. of California  
Davis, CA 95616



# A NEW *GENTIANA* (GENTIANACEAE) FROM NORTHERN CALIFORNIA AND SOUTHERN OREGON

CHARLES T. MASON, JR.

Herbarium, University of Arizona, Tucson, AZ 85721

## ABSTRACT

***Gentiana plurisetosa***, a new species from southern Oregon and northern California, is distinguished from other species by its multiciliate plicae associated with erect, glabrous stems.

In studies of highly variable genera, as *Gentiana*, one must guard against the tendency to describe each variation as a new taxon. There are, however, in northern California and southern Oregon several populations of a gentian that are sufficiently distinct to deserve recognition as a new species.

***Gentiana plurisetosa*** C. Mason, sp. nov. (Fig. 1)—TYPE: USA. California, Siskiyou Co: Marble Mountain Primitive area, Half Moon Meadow, 1670 m, 29 Aug 1939, C. C. and S. K. Harris 976 (holotype: ARIZ 29570, isotypes CAS, DS, MONTU, OSC, RM, UC, UTC, WIS, WS, WTU).

Herba perennis glabra. Caule ad 40 cm alti erecti. Folia ovata vel orbicularia, 2–6 cm longa. Flores vulgo multi interdum solitarii, terminales interdum in 1 vel 2 nodis summis, 4.5–5 cm longi, 2–2.5 cm lati. Calyx tubo 14–16 mm longo, lobis lanceolatis 10–14 mm longis. Corolla campanulata caerulea punctis viridibus, lobis 10–15 mm longis ovatis erosis; plicis bifidis cum setis 7–9 capillari-bus.

Glabrous perennial herbs with erect stems to 40 cm tall. Leaves ovate to orbiculate, fleshy, 5-veined, entire, 2–6 cm long, 2–3.5 cm wide, frequently longer than the internodes. Flowers 4–5 cm long, with 1–several at the apex or occasionally 1 or 2 nodes down, closely subtended by 2 narrow lanceolate, keeled bracts and frequently by 2 ovate to elliptical leaves. Calyx tube 14–16 mm long, thin membranous and commonly spathaceous, intracalycine membrane prominent; lobes lanceolate, 10–14 mm long. Corolla blue with green dots inside, 4–5 cm long, broadly campanulate; lobes rounded, 10–15 mm long, conspicuously erose. Plicae with 2 primary lobes; each lobe with 3–5 capillary setae 1.5–2 times as long as the corolla lobes. Stamens extrorse; anthers not united. Pistil at anthesis 1.5–2 cm long on a stipe 5–15 mm long.

*Representative specimens.* CA. Humboldt County: Trinity Sum-





FIG. 1. *Gentiana plurisetosa*. a, plant; b, open corolla; c, open calyx. Drawn from Mason 1789 (ARIZ).



mit, *Tracy* 5274 (JEPS, UC); *Kildale* 1194 (DS); *Jotter* 247 (CAS); N of Trinity Mts, *Esplin* 20 (CAS). Siskiyou County: Log Lake, Shackelford Creek, *Butler* 419 (JEPS, DS); *Butler* 1709 (JEPS, RM); English Lake, *Kildale* 6508 (DS); Western Salmon Mts., forest road crossing of Oregon Creek, *Niehaus* 935 (ARIZ, CAS, JEPS, RSA, US). OR. Josephine County: Bigelow Lakes, *Greenleaf* 1379 (OSC); Upper Bigelow Lake, *Baker and Ruhle* 665 (ID, WTU); *Mason* 1790 (ARIZ); *Applegate* 11467 (DS); Lower Bigelow Lake, *Baker and Ruhle* 603 (ID); *Mason* 1789 (ARIZ); Bog Cave Lake, *Peck* 8302 (OSC); Grayback Mountain, 1979, *Mansfield* s.n. (OSC); East side Grayback Mountain, O'Brien Creek, *Greenleaf* 1373 (OSC).

Through interpretations that expanded the specific limits of *G. setigera* A. Gray and *G. bisetata* Howell, *G. plurisetosa* has been overlooked as a distinct species. Gray (1876) in his characterization of *G. setigera* referred to the stems as ascending and described the plicae with "2–3 thin capillary setae which nearly equal the (corolla) lobes." His description includes "4 flowers at the apex," but the type specimen (GH) is immature and destroyed by insects so the number of flowers is difficult to determine. In later publications (Gray 1880, 1886) he modified the descriptions to indicate a single terminal flower. Howell (1901) did not recognize *G. setigera* but described *G. bisetata* as having decumbent stems, a solitary flower, and "appendages in the sinuses 2 setae from a rather broad base".

In more recent floristic literature Jepson (1925, 1939) and Munz (1959) recognized *G. setigera*. They acknowledged the ascending stems of *G. setigera*, but specified 1 to several flowers and 2 to several setae on the plicae. Abrams (1951) cited *G. setigera* with "2–8 capillary bristles about equalling the corolla lobes" and *G. bisetata* with "two capillary bristles about half the length of the corolla lobes." Both species are considered to have erect or ascending stems. Peck (1941) accepted *G. setigera* and considered *G. bisetata* a synonym. The plicae are described as having "several long fine setae," and the stems are decumbent with one terminal or 1–3 axillary flowers. In the second edition (Peck 1961) he dropped *G. setigera* and accepted *G. bisetata* with decumbent stems and solitary or 1–3 axillary flowers with 2 to several long fine setae. Chambers and Greenleaf (1989) have determined that *G. bisetata* should be recognized as a synonym of *G. setigera*.

*Gentiana plurisetosa* shows similarity to *G. setigera* in the large flowers with long corolla lobes, the capillary plicae, and glabrous stems and leaf margins. The ranges of leaf shapes of the two species overlap. In addition to the multiciliate plicae, it differs by having erect stems usually with several terminal flowers in contrast to the single flowered inflorescence on decumbent stems of *G. setigera*. *Gentiana plurisetosa* lacks the basal rosette of leaves commonly present in *G. setigera*, and it is found at elevations between 1230–1938 m, somewhat higher than the 340–1075 m of *G. setigera*.



*Gentiana oregana* Englem. ex A. Gray (*G. affinis* Griseb. var *ovata* A. Gray) is similar to *G. plurisetosa* in having large broadly funnelform to campanulate flowers arranged either as a few at the apex or extending down the stem 2 or 3 nodes. In *G. oregana* the plicae are bifurcated without capillary setae and are about  $\frac{1}{2}$  the length of the corolla lobes. The stems in the nodal areas are finely puberulent in rows as continuations of the minutely scabrous leaf margins, the upper internodes are about twice the length of the subtending leaf, and both the calyx and corolla lobes are approximately  $\frac{1}{2}$  the size of those of *G. plurisetosa*. *Gentiana oregana* is found at elevations ranging from 700–2215 m.

*Gentiana calycosa* Griseb., a widely distributed and highly variable species, is sometimes confused with *G. plurisetosa*. The two do not occur commonly in the same area, and *G. calycosa* is usually found at higher elevations. It also differs in having a single terminal flower on an ascending stem. The flowers are variable in size, but usually range between 3.5–4 cm long. The corolla lobes are entire or erose with acute or rounded apices, and range from 7–9 mm long. The plicae are 2 lobed, rarely 3 or 4 lobed, and attenuate, but not of capillary setae. They are  $\frac{1}{2}$  to  $\frac{3}{4}$  the length of the corolla lobes.

#### LITERATURE CITED

- ABRAMS, L. 1951. Illustrated flora of the Pacific states, Vol. 3. Stanford University Press, Stanford.
- CHAMBERS, K. L. and J. GREENLEAF. 1989. *Gentiana setigera* is the correct name for *G. bisetata*. Madroño 36:49–50.
- GRAY, A. 1876. Miscellaneous botanical contributions. Proc. Amer. Acad. Arts 11: 71–104.
- . 1880. Botany of California, Vol. I, 2nd ed. Gamopetalae, Geological survey of California. Little, Brown & Co., Boston.
- . 1886. Synoptical flora of North America, Vol. II, pt 1. Gamopetalae, 2nd ed. Ivison, Blakeman, Taylor & Co., New York.
- HOWELL, T. 1901. A flora of northwest America. fasc. IV:445.
- JEPSON, W. L. 1925. A manual of the flowering plants of California. Assoc. Students Store, Univ. of Calif., Berkeley.
- . 1939. A flora of California, Vol. 3, Part 1. Assoc. Students Store, Univ. of Calif., Berkeley.
- MUNZ, P. A. 1959. A California flora. Univ. of Calif. Press, Berkeley.
- PECK, M. E. 1941. A manual of the higher plants of Oregon. Binford & Mort, Portland.
- . 1961. A manual of the higher plants of Oregon, 2nd ed. Binford & Mort, Portland.

(Received 19 Oct 1989; revision accepted 22 May 1990.)



# *THELESPERMA CAESPITOSUM* (ASTERACEAE), A NEW SPECIES FROM WYOMING AND UTAH

ROBERT D. DORN  
Box 1471, Cheyenne, WY 82003

## ABSTRACT

*Thelesperma caespitosum*, a new species from Wyoming and Utah, is described and illustrated. The new species is a member of the *T. subnudum* complex and is compared to four related taxa. Possible evolution in the complex is discussed.

The Green River Formation in southwest Wyoming has always looked ideal to me as habitat for endemic species because of the extensive, barren, shale hills. Several endemics including *Lesquerella congesta* Rollins, *Lesquerella parviflora* Rollins, *Physaria obcordata* Rollins, and *Thalictrum heliophilum* Wilken & DeMott have been discovered recently on this formation in western Colorado, but none were previously found in Wyoming. In the spring of 1988 I encountered a small population of *Thelesperma* on this formation that I immediately recognized as different from known taxa in the genus.

***Thelesperma caespitosum* Dorn, sp. nov.** (Fig. 1)—TYPE: USA, Wyoming, Sweetwater Co., T18N R106W SE $\frac{1}{4}$  of SE $\frac{1}{4}$  of Sect. 31 and SW $\frac{1}{4}$  of SW $\frac{1}{4}$  of Sect. 32, 5 km SE of Green River, barren white shale ridge, 1890 m, 22 Jun 1988, *Dorn 4948* (holotype, RM; isotypes, to be distributed).

Perennis, radice lignosa, caudice ramoso, caulibus glabris 4–19 cm altis, foliis basalibus plerumque pinnatidivisis vel ternatidivisis, petiolis et interdum laminis ciliatis in marginibus, capitulis 1 vel raro 2, involucris 6–11 mm altis, ligulis nullis, corollis discis luteis (4–)5.5–9 mm longis, pappo nullo, achaeniis glabris (4–)4.8–7(–7.5) mm longis.

Perennial from a woody taproot and branched caudex that bears a dense series of persistent old leaf bases. Stems 4–19 cm high, glabrous, naked or with a few reduced leaves or bracts which are generally opposite below and alternate above. Leaves mostly basal, 1–6 cm long, pinnately or ternately divided into mostly 3–5 linear-elliptic segments which are sometimes again divided, segments mostly 1–2(–4) mm wide and 3–12(–18) mm long (or some leaves occasionally simple), glabrous except for ciliate petiole margins and sometimes blade margins (rarely entirely glabrous). Heads 1 or rarely 2; involucre 6–11 mm high, inner bracts with broad scarious margins, nearly free to connate about  $\frac{1}{3}$  their length, outer bracts linear



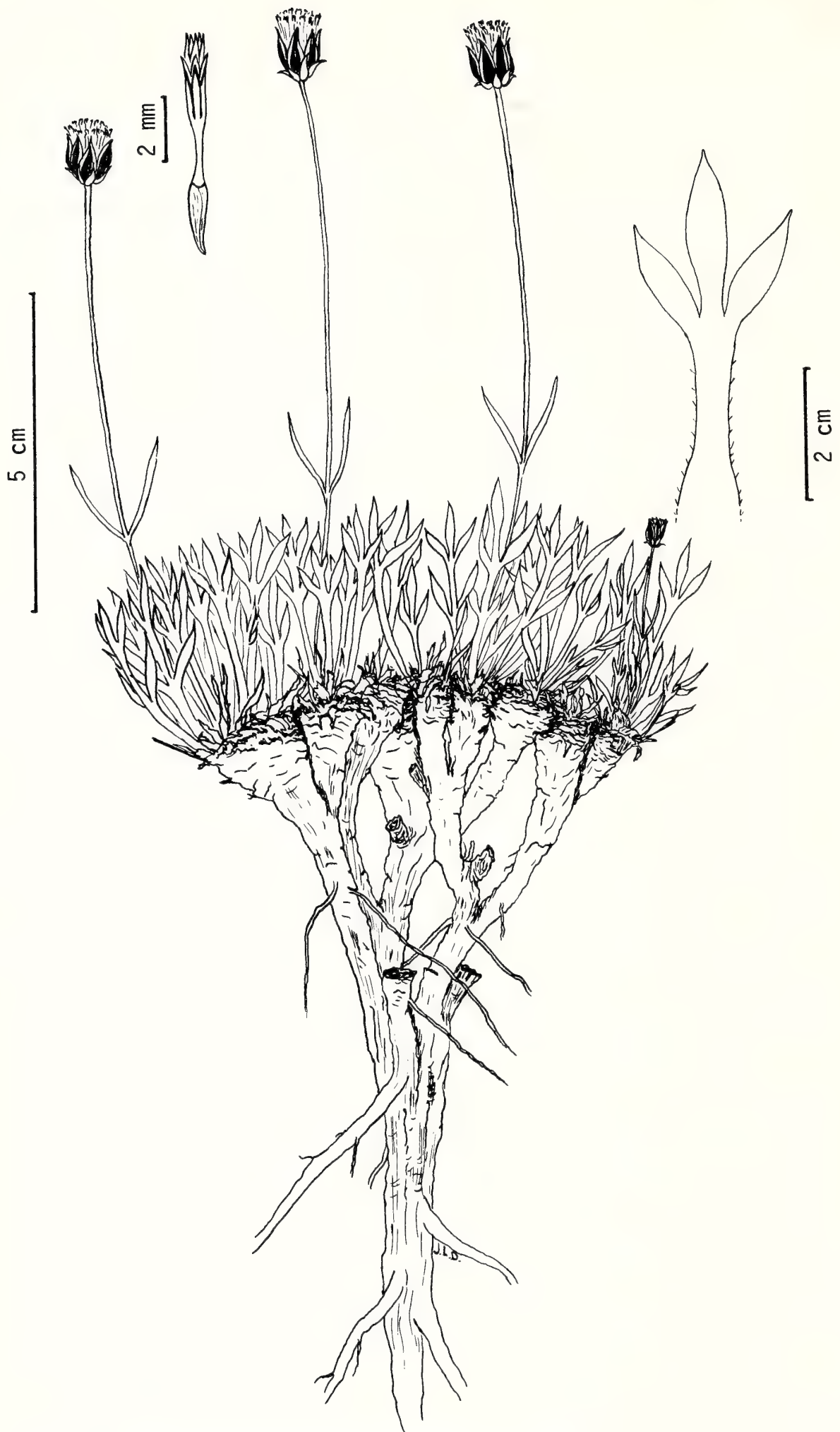


FIG. 1. *Thelesperma caespitosum* habit, flower, and leaf.



to lanceolate, about half as long as inner; ray flowers lacking; disk corollas yellow, (4–)5.5–9 mm long, with reddish-brown longitudinal veins that split at each corolla sinus and pair and meet with an adjacent vein at tip of corolla lobes, the lobes triangular and much shorter than throat; pappus lacking; achenes glabrous, mostly olive-brown, lance-linear and slightly curved, ridged on front and back faces and longitudinally striate, (4–)4.8–7(–7.5) mm long, each subtended by a longer membranous bract. Chromosome number unknown.

*Paratypes.* USA, Wyoming, same location as holotype, 31 May 1988, *Dorn 4941* (RM); Utah, Duchesne Co., SW of Duchesne, white shale benches, 1800 m, 15 Jun 1947, *Ripley and Barneby 8700* (NY).

*Thelesperma caespitosum* belongs to the *T. subnudum* complex which now consists of four species and one variety. Differences between the taxa are summarized in Table 1 and distribution of the taxa is shown in Figure 2. *Thelesperma subnudum* and *T. marginatum* are mostly tall, glabrous plants with relatively long and broad leaf segments, the rootstocks are somewhat creeping, and there are often several heads per stem. In contrast, *T. caespitosum* and *T. pubescens* are short plants with some pubescence, leaf segments are relatively short and narrow, the caudex is branched with a stout taproot, and there is usually 1(2) head per stem. The leaf pubescence in *T. caespitosum* is restricted to the petiole (rarely on lower blade), the herbage appears bright green in the field, and the achenes average 5 mm or more long [(4–)4.8–7(–7.5) mm]. In *T. pubescens*, the leaves are pubescent all over, the herbage often appears grayish in the field, and the achenes average less than 5 mm long [(3.8–)4–4.7(–5) mm]. *Thelesperma subnudum* var. *alpinum* seems to have evolved parallel to *T. caespitosum* and *T. pubescens* but has not diverged quite as far from *T. subnudum*. The divergence might be considered enough to warrant specific status, however. Since var. *alpinum* is the only member of the group for which I have no field experience, I hesitate to provide a definite opinion on its rank.

*Thelesperma subnudum* appears to be the ancestral species of the complex with its relatively widespread distribution, common habitat, mostly several heads per stem, and ray florets usually present. This likely gave rise to *T. marginatum* which also has a relatively widespread distribution but a more specialized habitat and a lack of ray florets. The two are now allopatric. *Thelesperma caespitosum* and *T. pubescens* may have evolved at the time *T. subnudum* and *T. marginatum* were diverging both geographically and genetically. More likely they were derived from *T. subnudum* at a later date. Their habitats are even more specialized than that of *T. marginatum*, their distribution is highly restricted, they have developed a much-branched caudex characteristic of desert vegetation, they have ac-



TABLE 1. SELECTED CHARACTERISTICS FOR TAXA OF THE *THELESPERMA SUBNUDUM* COMPLEX.

| Species or variety                                      | Leaf segments    | Pubescence                   | Heads                               | Rootstock  | Habitat                                   | Distribution                      |
|---|------------------|------------------------------|-------------------------------------|--|---|-----------------------------------|
| <i>T. subnudum</i> A. Gray<br>var. <i>subnudum</i>      | long,<br>broad   | none                         | 1-several,<br>ligulate<br>(discoid) | somewhat<br>creeping                                       | common, desert shrub                      | N AZ, N NM,<br>UT, W & S CO       |
| <i>T. marginatum</i> Rydb.                              | long,<br>broad   | none                         | 1-several,<br>discoid               | somewhat<br>creeping                                       | specialized,<br>rocky outwash             | SE ALTA, SW<br>SASK, MT, NW<br>WY |
| <i>T. caespitosum</i> Dorn                              | short,<br>narrow | on petioles<br>(lower blade) | 1(2), discoid                       | taproot,<br>branched<br>caudex                             | specialized,<br>white shale               | NE UT, SW WY                      |
| <i>T. pubescens</i> Dorn                                | short,<br>narrow | on leaves                    | 1(2), discoid                       | taproot,<br>branched<br>caudex                             | specialized,<br>weathered<br>conglomerate | SW WY                             |
| <i>T. subnudum</i> A. Gray<br>var. <i>alpinum</i> Welsh | short,<br>narrow | on leaves &<br>lower stems   | 1(2), discoid                       | somewhat<br>creeping<br>to taproot &<br>branched<br>caudex | specialized,<br>sandy?                    | SC UT                             |



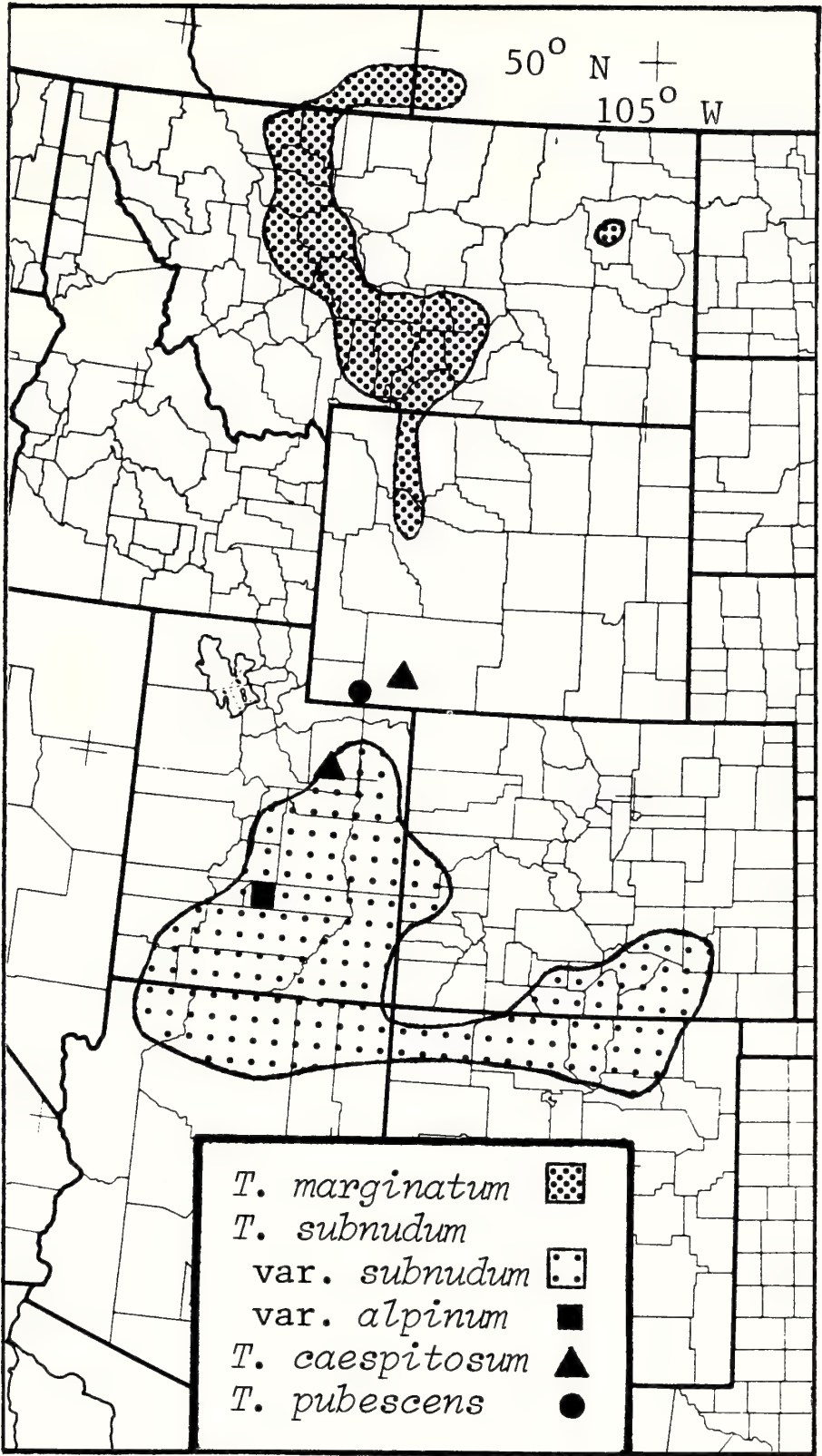


FIG. 2. Central and southern Rocky Mountain region of western North America showing distribution of taxa in the *Thelesperma subnudum* complex.

quired pubescence, the leaves have been reduced, and the heads have been reduced to one or rarely two per stem. It is likely that *T. pubescens* arose from *T. caespitosum* or vice-versa, or they may have arisen simultaneously from *T. subnudum*. *Thelesperma subnudum*



var. *alpinum* appears to be a later derivative parallel to *T. pubescens* and *T. caespitosum*, but it is not yet as stable as these taxa. Narrow endemics in this region tend to exploit severe habitats where there is little or no competition, and that is the pattern followed by *T. pubescens* and *T. caespitosum* and to a lesser extent by *T. subnudum* var. *alpinum*. In most cases, these endemics appear to be relatively recently evolved rather than relicts as reflected in their specialized adaptations for coping with a severe environment. Older environments were more moderate.

#### KEY TO TAXA IN THE *THELESPERMA SUBNUDUM* COMPLEX

- A. Plants usually glabrous; heads 1 to several per stem; rootstock somewhat creeping, lacking a much branched caudex with persistent old leaf bases.
  - B. Heads with both ray and disk flowers, rays rarely lacking; Arizona, New Mexico, Utah, and Colorado . . . . . *T. subnudum* A. Gray var. *subnudum*
  - B' Heads with only disk flowers, rays lacking; Alberta, Saskatchewan, Montana, and NW Wyoming . . . . . *T. marginatum* Rydb.
- A' Plants pubescent at least on petioles (very rarely glabrous); heads 1 or rarely 2 per stem; rootstock generally with a much branched caudex with many persistent old leaf bases.
  - C. Flower stems pubescent at least on lower portion; SC Utah . . . . . *T. subnudum* A. Gray var. *alpinum* Welsh
  - C' Flower stems glabrous; NE Utah and SW Wyoming.
    - D. Leaves pubescent throughout . . . . . *T. pubescens* Dorn
    - D' Leaves pubescent only on petioles (rarely on lower blade) . . . . . *T. caespitosum* Dorn

#### ACKNOWLEDGMENTS

I thank Ronald Hartman, curator of RM, for use of those facilities, and the reviewers of the original manuscript, including Arthur Cronquist, Thomas Melchert, and David Keil, for their helpful comments. Cronquist also brought the Ripley and Barneby collection to my attention and I thank the curator of NY for the loan of several specimens.

(Received 18 Jan 1989; revision accepted 22 May 1990).



A NEW SUBSPECIES OF *CIRSIIUM PARRYI*  
(ASTERACEAE: CARDUEAE) FROM ARIZONA AND  
COMMENTS ON THE *CIRSIIUM PARRYI* COMPLEX

C. G. SCHAACK

Department of Botany, University of Wisconsin,  
Madison, WI 53706

GREGORY A. GOODWIN

Coconino National Forest, 2323 Greenlaw Lane,  
Flagstaff, AZ 86004

ABSTRACT

*Cirsium parryi* subsp. *mogollonicum* is applied to a local variant of *Cirsium parryi* discovered on the Mogollon Escarpment, Arizona. The white fresh corollas and nearly entire basal and cauline leaves of this understory, canyon dwelling subspecies distinguish it from the other members of the *C. parryi* complex that includes the Wooton and Standley segregates, *C. gilense*, *C. inornatum*, and *C. pallidum*, of wet meadows/parklands. Mature leaves of *C. parryi* subsp. *parryi* and the Wooton and Standley segregates are sinuately toothed to sinuately lobed and corollas are described as yellow-ochroleucous. Type material of *Cirsium gilense* and *C. inornatum* appears to differ little from variation noted in *C. parryi* subsp. *parryi* and perhaps should again be submerged within *C. parryi*. The relatively long, linear, densely pubescent tips of the outer and middle phyllaries noted on the holotype of *Cirsium pallidum* serve to distinguish this taxon from others in the complex.

During a field trip on 7 July 1987 to survey riparian vegetation along the perennial streams on the Mogollon Rim that ultimately drain northward to the Little Colorado River, we discovered an unusual *Cirsium* in late bud within the cool, shaded confines of the canyon cut by Dane Spring. Later in the season this thistle was located in the streamside understory of Dane Canyon just upstream from the confluence of Dane and Dane Spring Canyons. Three riparian vegetation inventories have been completed in canyons adjacent to Dane and Dane Spring Canyons since 1987 and this *Cirsium* is still known only from the original sites of discovery.

The white fresh corollas and nearly continuous, spinulose-ciliate margins of the basal and cauline leaves of this *Cirsium* did not immediately suggest any known Arizona species (Kearney and Peebles 1960). Because the corollas dried a very light yellow, we borrowed material of the yellow flowered *Cirsium parryi* (A. Gray) Petrak (Petrak 1911) from ARIZ. Observed similarities in phyllary morphology established between these specimens and the Dane Spring Canyon thistle prompted us to borrow type specimens of the basionym of *Cirsium parryi*, *Cnicus parryi* A. Gray (Gray 1874), [GH,



ISC, NY, and US] and a sampling of specimens [MIN] from throughout the range of *C. parryi* (Harrington 1954; Martin and Hutchins 1980; Kearney and Peebles 1960) as well as type material of the yellow flowered thistles once included within *C. parryi* (Wooton and Standley 1913): *C. gilense* Wooton and Standl., *C. inornatum* Wooton and Standl., and *C. pallidum* Wooton and Standl. (US).

Phyllary and corolla morphology observed in our thistle closely resembles that found in *C. parryi* subsp. *parryi*, *C. gilense*, and *C. inornatum*. Phyllaries with dilated, scarious-coriaceous, lacerate-fimbriate tips, common to all others in the *C. parryi* complex, are missing in *Cirsium pallidum*. Tips of the outer phyllaries on the holotype of *C. pallidum* are long, nearly linear, and densely pubescent, primarily at the margins, with coarse moniliform hairs (Wooton and Standley 1913). Both tip length and pubescence decrease as the innermost whorl of phyllaries is approached. The innermost whorl of bracts is similar morphologically to those found elsewhere in the *C. parryi* complex. *Cirsium gilense* and *C. inornatum* were segregated from *C. parryi* (Wooton and Standley 1913) based on characters that vary greatly throughout the *C. parryi* complex: head size, head number per branch, number of foliaceous bracts below the head, leaf thickness, and leaf spininess. On annotations applied to specimens in 1967, R. J. Moore commented on the poorly defined nature of *C. gilense*, *C. inornatum*, and *C. pallidum*, "New Mexico plants related to *C. parryi* are said to be either *C. pallidum*, *C. gilense* or *C. inornatum*. The distinction is difficult." Except as indicated for *C. pallidum* above, we agree with Moore and suggest that variation included within *C. gilense* and *C. inornatum* could be comfortably housed within *C. parryi* subsp. *parryi*. No new status is offered, or suggested, for *C. pallidum*.

Phyllary and corolla morphology of the Dane Spring and Dane Canyon *Cirsium* indicate that it has had its origin from within the *C. parryi* complex. On the other hand, the white fresh corollas and nearly continuous basal and cauline leaf margins of our thistle contrast strongly with the yellow-ochroleucous corollas and sinuate-dentate to sinuately lobed leaves reported for the rest of the complex. Spines of this thistle are poorly developed and similar, in stoutness and size (normally 2 mm or less in length), to those found on very immature (juvenile) leaves of *C. parryi*. Unlike other members of the complex that are adapted to wet mountain meadows and parkland, the Dane Spring and Dane Canyon *Cirsium* is restricted to the low light intensities of the canyon understory. We believe that the thistle we discovered represents variation unique within *C. parryi* and we here propose a new subspecies.

***Cirsium parryi* subsp. *mogollonicum*** C. Schaack & G. Goodwin subsp. nov. (Fig. 1)—TYPE: USA, Arizona, Coconino Co., Mogollon



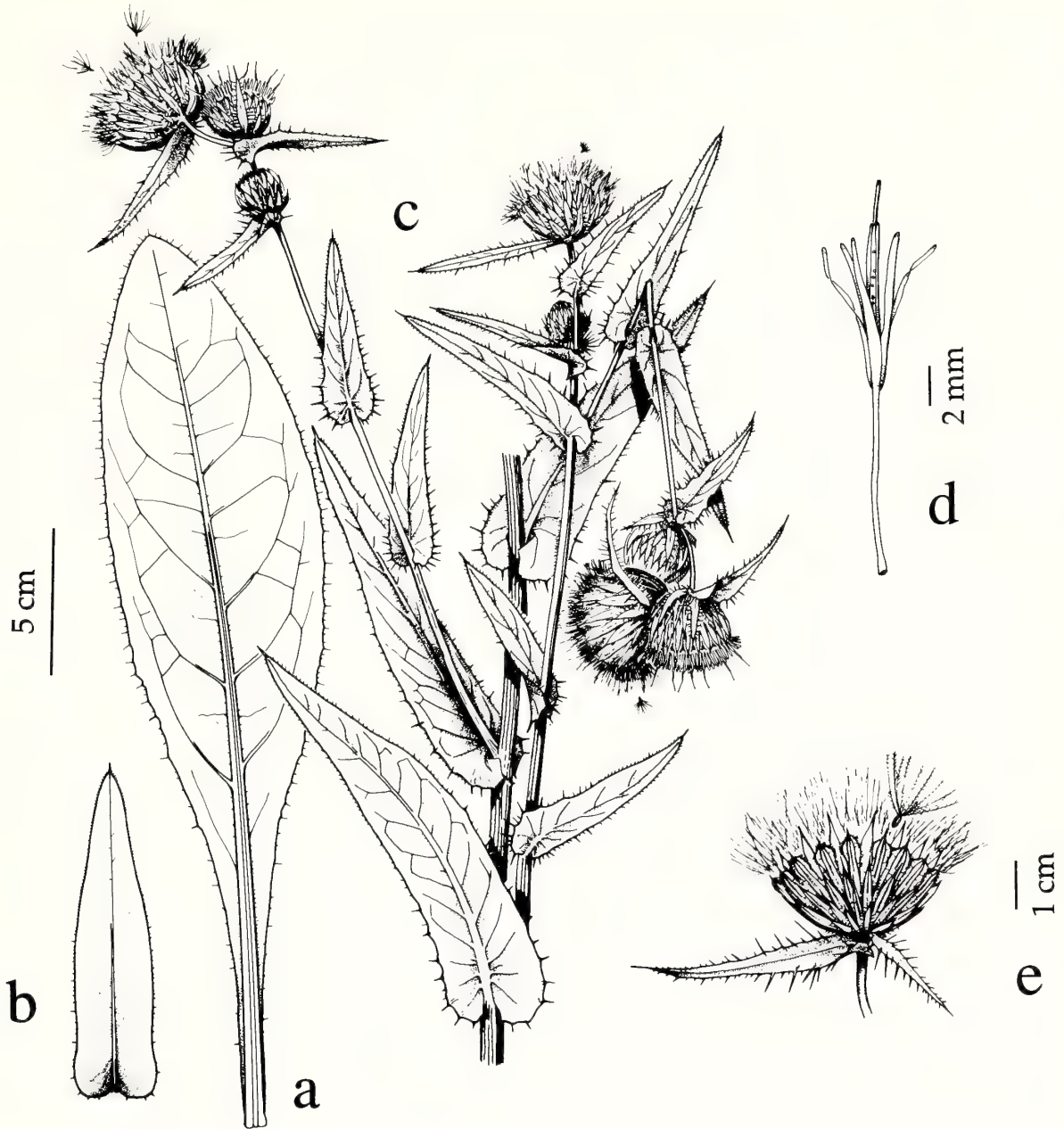


FIG. 1. *Cirsium parryi* (A. Gray) Petrak subsp. *mogollonicum* Schaack and Goodwin (drawn from the holotype and isotype Schaack et al. 2175 and paratype Schaack et al. 2241). a, Basal leaf; b, lower cauline leaf; c, head-bearing branches; d, corolla; e, head.

Rim, riparian habitat, shaded confines of Dane Spring Canyon, T13N R11E sect. 35, ca. 2195 m (7200 ft), 27 Aug 1987, Schaack et al. 2175 (holotype, WIS; isotype, ARIZ).

Corolli dulces albi et margines foliorum basaliū et caulīnorum principalium paene continui, tantum interrupti spinis minutis 2 mm longis vel brevioribus distinguunt subsp. *mogollonicum* a subsp. *parryi* corollis ochroleucis vel flavis et marginibus foliorum sinuate dentatis vel lobatis spinis plerumque longioribus quam 2 mm.

Taprooted biennial (short-lived perennial?), 0.55–1.52(–2.0) m tall. Stems normally branched only at or near the apex, basally



hollow and succulent, ribbed, thinly-densely arachnose below the heads, otherwise villous-glabrous; nodes of the unbranched stem 3.0–7.5 cm apart. Rosette leaves broadly spatulate, sparingly pilose and darker green above, glabrate and lighter green below, margins spinulose ciliate, otherwise continuous. Cauline leaves alternate, the first few oblanceolate-spatulate, the remainder lanceolate-broadly lanceolate, sessile and clasping with more or less rounded auricles, not decurrent, short and weakly spine-tipped apically (ca. 2 mm), darker green and thinly pubescent above, glabrate and lighter green beneath; margins of leaves positioned below those subtending the head bearing branches spinuliferous-spinulose ciliate (spines ca. 2 mm or < in length) otherwise undissected, margins of leaves and bract-like leaves on or subtending the head-bearing branches also nearly continuous but more heavily armed. Heads solitary, or few (2–4), borne at the stem apex or on branches that arise from the upper leaf axils, subtended by spiny, bract-like leaves that grade from bracts large enough to overtop the heads to those that are similar in size and shape to the phyllaries. Involucres at anthesis thinly arachnose, 1.6–2.0 cm high, 2.0–2.7 cm across; phyllaries loosely imbricate, in few series, without a dorsal glutinous ridge; outer phyllaries lanceolate, spine-tipped, scabrellate dorsally and at margins for  $\frac{1}{3}$ – $\frac{1}{2}$  of their length, otherwise chartaceous fimbriate, some spinulose ciliate at the base; middle phyllaries more or less lanceolate, weakly spine-tipped with a dilated apex, scabrellate dorsally and at the margins for most of their length, margins of the dilated tip scarious-chartaceous, lacerate-fimbriate; innermost phyllaries narrowly lanceolate, weakly spine-tipped to short aristate, ciliate-fimbriate to nearly entire at the narrowed apex, scabrellate dorsally and at the margins below. Corollas white when fresh, drying a very light yellow, 10–14 mm long; the tube 8.0–10.0 mm long; the throat 2.0–4.0 mm long, (0.7–)1.0–1.5(–1.75) mm wide; lobes nearly equal, linear-lanceolate, 4.0–6.0 mm long; pappus plumose, dusky white-light brown in dried specimens. Achenes flat, light brown and black streaked to nearly black, 5.0–5.1 mm long, 1.9–2.25 mm wide; fruiting pappus 12–13 mm long.

*Paratypes.* USA, Arizona, Coconino Co., Mogollon Rim, Dane Canyon in the understory just upstream from the confluence of Dane and Dane Spring Canyons, T13N R11E sect. 35, ca. 7200 ft (2195 m) 27 Aug 1987, *P. Boucher* 662 (ASC); 12 Sep 1987 *C. Schaack et al.* 2241 (ASU); 100 yards south of the junction of Dane Spring Canyon and Dane [in Dane Canyon], grassy area below Douglas-fir, 30 Sept 1989, *William Knight s.n.* (ASU, OBI).

#### KEY TO THE *CIRSIUM PARRYI* COMPLEX

- A. Phyllary tips of outer and middle bracts nearly linear, without dilated tips; densely pubescent, primarily at the margins, with coarse moniliform hairs . . . . *C. pallidum*



- A' Phyllaries between the outermost and innermost bract series with dilated, scarious-chartaceous, lacerate-fimbriate tips; tips lacking coarse moniliform hairs . . . . B
- B. Corollas yellow-ochroleucous; mature cauline and/or basal leaves sinuately toothed-sinuately lobed and armed at the margins with spines normally >2 mm long; plants of moist or wet ground in mountain meadows and parkland, Arizona, Colorado, New Mexico, and Utah (Welsh et al. 1987). . . . . *C. parryi* subsp. *parryi*
- B' Fresh corollas white; margins of mature leaves beset with spines ca. 2 mm long or < [spinulose ciliate] otherwise continuous; plants of moist to very moist soils in the riparian understory of Dane Spring and Dane Canyons, Mogollon Escarpment, Arizona . . . . . *C. parryi* subsp. *mogollonicum*

*Distribution, habitat and phenology.* *Cirsium parryi* subsp. *mogollonicum* is a rare thistle (ca. 40 individuals) and is restricted in Arizona to less than one square mile of equally rare habitat: associated with perennial streams above 7000 feet (2134 m). Though a small portion of the Dane Spring and Dane Canyon *Cirsium* population occurs under somewhat open coniferous canopy [*Pinus ponderosa* Dougl., *Pseudotsuga menziesii* (Mirbel) Franco and *Abies concolor* (Gordon & Glendinning) Lindl.], it occurs more typically under nearly closed canopy and/or within narrow canyon confines where direct sunlight is limited, or nearly excluded, for much of the day. In the latter situation, associates include: *Aquilegia triternata* Payson, *Aralia racemosa* L., *Athyrium filix-femina* (L.) Roth, *Dryopteris filix-mas* (L.) Schott, *Sambucus microbotrys* Rydb. and *Sorbus dumosa* E. Greene. Anthesis of this *Cirsium* begins in July and continues into September. We observed individuals of *Bombus* working the flowers in August. This poorly armed thistle is subject to browsing, apparently by elk. Though evidence of browsing was not noticed in our 1987 collections, the 1989 collections of *C. parryi* subsp. *mogollonicum* by Knight showed signs of this activity. Normally only the first few nodes of this thistle, when uncropped, bear spatulate-oblongate leaves. Leaves above these nodes are normally lanceolate. New growth from the cropped paratypes of Knight differed from this pattern and held many more spatulate-oblongate leaves than uncropped plants.

The *Cirsium* we report is not the only unusual find in the riparian habitat of the canyons flowing northward to the Little Colorado. To further emphasize the singular nature of these environs, Dane Canyon, upstream from the *Cirsium* site, houses the second, and perhaps now the only, known Arizona location for the circumboreal fern species *Gymnocarpium dryopteris* (L.) Newm. (Boucher 1988). Additionally, the canyon sides above the site of the type collection of *C. parryi* ssp. *mogollonicum* support a small population of *Vaccinium myrtillus* L., previously known only from higher elevations in the White Mountains of eastern Arizona (Kearney and Peebles 1960) and the San Francisco Mountain near Flagstaff (ASC). Orchids, *Platanthera limosa* Lindl. and *Listera convallarioides* (Sw.) Nutt., re-



ported only from the mountains of southern Arizona (Kearney and Peebles 1960) occur just downstream in Dane Spring Canyon from the *Cirsium* and *Vaccinium* locality. Arizona's largest population of *Polystichum lonchitis* (L.) Roth (Michael Windham pers. comm.) also occurs in Dane Spring Canyon. Additional discoveries will be included in a riparian flora of these canyons, in preparation, by Goodwin et al. At this writing, this endemic subspecies and the unique Arizona habitat in which it grows are not endangered. Clearly, careful consideration should be given to protecting high altitude perennial stream habitat within Arizona, a rare and valuable natural resource.

#### ACKNOWLEDGMENTS

We are grateful to the curators at ARIZ, GH, ISC, MIN, NY, and US for the loan of specimens and/or type material. The Biology Department of Northern Arizona University and Dr. James Rominger, the former curator of ASC, are acknowledged for the facilities provided at the beginning of this project. Dr. David J. Keil prepared the Latin diagnosis, and Kandis Elliot the fine illustration. Plate photography was by Claudia Lipke. The comments of Drs. David Keil, Donald Pinkava, and Gerald Ownbey on a previous draft were appreciated. Lastly, the senior author thanks the junior author for the introduction to the botanical wonders of Dane Spring Canyon.

#### LITERATURE CITED

- BOUCHER, P. 1988. Rediscovery of *Gymnocarpium dryopteris* in Arizona. Amer. Fern J. 78:39.
- GRAY, A. 1874. A synopsis of the North American thistles. Proc. Amer. Acad. Arts 10:39-48.
- HARRINGTON, H. D. 1954. Manual of the plants of Colorado. Sage Books, Denver, Colorado.
- KEARNEY, T. H. and R. H. PEEBLES. 1960. Arizona flora. Univ. Calif. Press, Berkeley and Los Angeles.
- MARTIN, W. C. and C. R. HUTCHINS. 1980. A flora of New Mexico. J. Cramer, Germany.
- PETRAK, F. 1911. Beitrage zur Kenntniss der Mexikanischen und Zentral-Amerikanischen Cirsien. Bot. Tidsskr. 31:57-72.
- WELSH, S. L. et al. 1987. A Utah flora. Great Basin Naturalist Memoir no. 9. Brigham Young University, Provo, Utah.
- WOOTON, E. O. and P. C. STANDLEY. 1913. Descriptions of new plants preliminary to a report upon the flora of New Mexico. Contrib. U.S. Natl. Herb. 16(4):195-196.

(Received 11 Jul 1989; revision accepted 6 Aug 1990.)



# A NEW SUBSPECIES OF *CLARKIA CONCINNA* (ONAGRACEAE) FROM MARIN COUNTY, CALIFORNIA

G. A. ALLEN

Department of Biology, University of Victoria, Victoria,  
B.C., V8W 2Y2, Canada

V. S. FORD and L. D. GOTTLIEB

Department of Genetics, University of California,  
Davis, CA 95616

## ABSTRACT

A new self-pollinating subspecies, *Clarkia concinna* subsp. *raichei*, is described from the California coast north of San Francisco Bay. It is interfertile with the other subspecies, *C. concinna* subsp. *concinna* and subsp. *automixa*, but differs in having less deeply lobed petals, more completely united sepals, shorter stature, and earlier flowering time.

*Clarkia* (Onagraceae) exhibits a diverse array of floral morphologies and petal pigmentation patterns (MacSwain et al. 1973; Gottlieb 1989). Some of the most unusual flowers in the genus are found in section *Eucharidium* Lewis & Lewis, which includes *C. concinna* (Fischer & C. Meyer) E. Greene and *C. breweri* (A. Gray) E. Greene (Lewis & Lewis 1955). These two species are characterized by large trilobed petals, four rather than eight stamens, and a long floral tube that adapts them to pollination by long-tongued Lepidoptera or Diptera (MacSwain et al. 1973). *Clarkia concinna* occurs in northern and western California from Del Norte to Butte and Santa Clara Counties. The widely distributed, outcrossed subsp. *concinna* has large showy flowers, is protandrous, and has a very long style with the stigma exerted well beyond the anthers. Smaller-flowered, self-pollinated populations from the South Coast Ranges, which lack protandry and have anthers positioned adjacent to the stigma, have been described as subsp. *automixa* (Bowman 1987). A new subspecies, also self-pollinated but differing from subsp. *automixa* in stature and in floral morphology, is described here.

## METHODS

Plants were grown from seed obtained from five populations of the three subspecies of *C. concinna*. Collections and localities were: subsp. *raichei*, Allen and Ford 1239 (type locality); subsp. *automixa*, Gottlieb 8701 (Santa Clara Co., Stevens Canyon Rd) and Gottlieb 8702 (Santa Clara Co., Soda Springs Canyon Rd); subsp. *concinna*,





FIG. 1. Representative flowers of *Clarkia concinna*: c = subsp. *concinna* (Gottlieb 8740), a = subsp. *automixa* (Gottlieb 8701), r = subsp. *raichei* (Allen and Ford 1239).

Gottlieb 8740 (Sonoma Co., Hwy 128 w of Conn Dam) and *Weeden 146* (Marin Co., 0.8 km W of summit, Lucas Valley Rd). One collection (*Weeden 146*, subsp. *concinna*) was obtained by random cross-pollination of 6–7 plants derived from the original field-collected seed; all other seeds were from field-collected populations. Seeds were germinated in moistened vermiculite, transplanted into 2-inch pots, and grown to flowering size in the greenhouse. Mature fully expanded petals and other floral parts were measured on at least 40 flowers from 20 plants of each population. Herbarium specimens at DAV, UC, JEPS, and CAS were also examined, to confirm conclusions reached from measurements made on these populations.

Pairwise crosses were made between individuals of each subspecies, and pollen stainability in lactophenol-aniline blue was determined in the parents and in the  $F_1$  hybrids to estimate infertility. Chromosome counts for subsp. *raichei* were made from root tips of newly germinated seedlings fixed in 3:1 ethanol:acetic acid and stained with leuco-basic fuchsin as described by Allen (1984).

## RESULTS

The most conspicuous morphological differences among the flowers of the three subspecies are summarized in Table 1. *Clarkia concinna* subsp. *raichei* and subsp. *automixa* both possess floral attributes associated with self-pollination: relatively small petals, anthers at the same height as the stigma, and absence of protandry. The



TABLE 1. FLORAL CHARACTERS OF THE THREE SUBSPECIES OF *CLARKIA CONCINNA*, DETERMINED FROM POOLED SAMPLES OF PLANTS GROWN FROM SEED. Overall means and standard deviations are calculated from means for individual plants; ranges are the extremes found for individual flowers. Anther-to-stigma distance = style length - (filament length + floral tube length). All units are mm.

|                           | Subsp. <i>concinna</i> |           | Subsp. <i>automixa</i> |           | Subsp. <i>raichei</i> |           |
|---------------------------|------------------------|-----------|------------------------|-----------|-----------------------|-----------|
|                           | $\bar{x} \pm SD$       | Range     | $\bar{x} \pm SD$       | Range     | $\bar{x} \pm SD$      | Range     |
| Petal length              | 25.4 $\pm$ 2.5         | 19.0-30.5 | 18.4 $\pm$ 2.0         | 13.5-23.5 | 19.4 $\pm$ 0.6        | 17.5-21.5 |
| Midlobe length            | 10.5 $\pm$ 1.5         | 7.5-14.0  | 5.6 $\pm$ 1.0          | 2.5-8.5   | 2.9 $\pm$ 0.4         | 1.0-4.5   |
| Lateral lobe length       | 7.2 $\pm$ 1.2          | 4.5-9.5   | 3.0 $\pm$ 0.6          | 1.0-5.0   | 1.2 $\pm$ 0.4         | 0-2.5     |
| Style length              | 30.0 $\pm$ 2.0         | 25.5-34.0 | 24.7 $\pm$ 1.8         | 19.0-29.5 | 24.6 $\pm$ 0.9        | 22.0-27.0 |
| Floral tube length        | 17.3 $\pm$ 1.5         | 13.0-21.0 | 15.8 $\pm$ 1.3         | 11.5-20.0 | 14.6 $\pm$ 0.3        | 13.5-15.5 |
| Anther-to-stigma distance | 4.5 $\pm$ 1.2          | 1.5-7.0   | 0.6 $\pm$ 1.2          | 0-5.5     | 1.0 $\pm$ 0.5         | 0-2.5     |
| Midlobe/total length      | 0.41 $\pm$ 0.03        | 0.33-0.50 | 0.30 $\pm$ 0.04        | 0.16-0.45 | 0.15 $\pm$ 0.02       | 0.06-0.22 |



TABLE 2. POLLEN VIABILITY OF SUBSPECIES OF *CLARKIA CONCINNA* AND THEIR F<sub>1</sub> HYBRIDS. Determinations were made from 500 pollen grains per plant.

| Taxon or F <sub>1</sub> hybrid           | Number of plants sampled | Percent stainability of pollen ( $\bar{x} \pm \text{SD}$ ) |
|--|--------------------------|--|
| <i>automixa</i> (Gottlieb 8701)          | 5                        | 96.9 $\pm$ 2.4   |
| <i>concinna</i> (Gottlieb 8740)          | 6                        | 96.9 $\pm$ 1.8   |
| <i>raichei</i> (Allen and Ford 1239)     | 6                        | 95.9 $\pm$ 1.8   |
| <i>automixa</i> $\times$ <i>raichei</i>  | 5                        | 80.4 $\pm$ 4.3   |
| <i>raichei</i> $\times$ <i>automixa</i>  | 6                        | 77.5 $\pm$ 6.0   |
| <i>concinna</i> $\times$ <i>automixa</i> | 4                        | 73.0 $\pm$ 0.7   |
| <i>concinna</i> $\times$ <i>raichei</i>  | 9                        | 77.2 $\pm$ 1.6   |
| <i>raichei</i> $\times$ <i>concinna</i>  | 3                        | 81.9 $\pm$ 3.1   |

petals of subsp. *raichei* are similar in overall length to those of subsp. *automixa*, but have much shorter middle and lateral lobes (Table 1, Fig. 1). In subsp. *raichei* the middle lobe of the petals typically constitutes 10–20% of the total length, and the lateral lobes are often indistinct on one or more petals; in subsp. *automixa* the middle lobe of the petal generally constitutes 20–40% of total petal length, and the lateral lobes are well-marked and separated from the middle lobe by deep sinuses. The shape of the middle lobe is also an important distinguishing feature. The maximum width of the middle petal lobe relative to the width at the “neck” of the lobe is greatest in subsp. *concinna*, intermediate in subsp. *automixa*, and smallest in subsp. *raichei* (Fig. 1). In subsp. *concinna* and to some extent in subsp. *automixa*, the middle lobe of the lower petal of each flower curves upward, possibly directing the angle of approach of pollinators. This trait is absent in subsp. *raichei*.

The dimensions given in Table 1 are representative for early to mid-season flowers on healthy well-grown plants. However, petal size in *C. concinna* is affected by environment, flower position, and plant phenological stage. We observed smaller petals on late flowers, on laterally positioned flowers, and on small plants. Bowman (1987) gave a petal length of 8–12(–17) mm for subsp. *automixa*; this is often typical of field-collected subsp. *raichei* also, but under favorable conditions both subspecies have much larger petals (Table 1).

The subspecies also differ in other characteristics. In subsp. *raichei*, the relatively short, broad sepals are deflexed  $< \frac{1}{3}$  of the distance from the base, and are united for the upper  $\frac{2}{3}$  of their length to give the “boat-shaped” calyx characteristic of many other species of *Clarkia*. In the other two subspecies, the sepals are longer and narrower, deflexed at or just below the midpoint, and united only near the tip. The subspecies also differ in overall growth form; subsp. *raichei* is compact and usually less than 1 dm tall, whereas vigorous



plants of subsp. *automixa* and subsp. *concinna* are generally much taller.

Vigorous  $F_1$  progenies were obtained from all combinations of parental subspecies. In comparison with the parents,  $F_1$  plants showed a moderate decrease of 14% to 24% in percentage of stainable pollen (Table 2), suggesting relatively little genetic divergence. *Clarkia concinna* subsp. *raichei* is diploid, with the same chromosome number ( $2n = 14$ ) as in other taxa of section *Eucharidium*. The subspecies evidently differ little in chromosome arrangement, the most frequent cause of hybrid sterility between *Clarkia* species (Lewis 1973). The  $F_1$  plants were fertile, and most were able to set substantial amounts of seed by self-pollination.

### CONCLUSIONS

*Clarkia concinna* subsp. *raichei* is a localized self-pollinating race of *C. concinna* that is morphologically and geographically distinct from subsp. *automixa*, and probably arose separately from it.  $F_1$  hybrids between all pairs of the three subspecies show a similar decrease in pollen fertility, suggesting that genetically the three taxa are about equally divergent from one another. Their infertility indicates that they are not separated by any major chromosome rearrangement. *Clarkia concinna* subsp. *raichei* is an early-flowering plant of dwarf stature that occurs in exposed habitats, and is presently known only from a single locality in Marin County. No other populations of this subspecies have been found, although subsp. *concinna* occurs nearby, in less exposed habitats further inland. We have designated the new taxon subsp. *raichei* in honor of Roger Raiche (Botanical Garden, University of California, Berkeley), who discovered it.

### TAXONOMY

***Clarkia concinna*** (Fischer & C. Meyer) E. Greene subsp. ***raichei*** G. Allen, V. Ford & L. Gottlieb, subsp. nov.—TYPE: California, Marin Co., 1.1 km S of Tomales on Hwy 1, on steep NW-facing talus slope between milepost markers 43.88 and 44.40, 13 Apr 1988, *Allen and Ford 1239* (holotype, DAV; isotypes, JEPS, MO, RSA).

Flores non proterandri; petala 10–22 mm longa, parvilobata, lobo medio 1–4 mm longo, lobis lateralibus brevioribus interdum indistinctis; sepala in parte  $\frac{2}{3}$  distali deflexa connata.

Annual, stems ascending to erect, 0.5–2 dm tall, often branched. Leaves elliptic to ovate, 1–3 cm long, 5–10 mm wide, entire, reddish beneath. Flowers erect in bud, sessile. Sepals narrowly lanceolate,



8–14 mm long, 1–1.5 mm wide, deflexed  $\frac{1}{4}$  to  $\frac{1}{3}$  of distance from base, remaining united for upper  $\frac{2}{3}$  of length. Petals bright pink, 10–22 mm long, with three short lobes, the middle lobe 1–4 mm, the lateral lobes often present only as a shoulder on the middle lobe. Stamens 4, approximately equal, surrounding the style. Stigma obscurely 4-lobed, receptive as anthers mature. Chromosome number  $2n = 14$ .

#### ACKNOWLEDGMENTS

We are grateful to Kenton L. Chambers for assistance with the Latin diagnosis.

#### LITERATURE CITED

- ALLEN, G. A. 1984. Morphological and cytological variation in the western North American *Aster occidentalis* complex (Asteraceae). *Syst. Bot.* 9:175–191.
- BOWMAN, R. N. 1987. *Clarkia concinna* subsp. *automixa* (Onagraceae), a new subspecies from the South Bay region, central California. *Madroño* 34:41–47.
- GOTTLIEB, L. D. 1989. Floral pigmentation patterns in *Clarkia* (Onagraceae). *Madroño* 36:1–8.
- LEWIS, H. 1973. The origin of diploid neospecies in *Clarkia*. *Amer. Naturalist* 107: 161–170.
- and M. E. LEWIS. 1955. The genus *Clarkia*. *Univ. Calif. Publ. Bot.* 20:241–392.
- MACSWAIN, J. W., P. H. RAVEN, AND R. W. THORP. 1973. Comparative behavior of bees and Onagraceae. IV. *Clarkia* bees of the western United States. *Univ. Calif. Publ. Entom.* 70:1–80.

(Received 28 Feb 1990; revision accepted 6 Aug 1990.)



## NOTES

HERBARIA OF NEW MEXICO.—One of the last states to be explored botanically, New Mexico's first plant specimens were collected in the 1830's (McKelvey, Botanical exploration of the Trans-Mississippi West, 1955). Poorly explored areas still exist in the state.

Moreover, the present size of herbarium collections in New Mexico is markedly smaller than that of neighboring states, in spite of the great diversity in topography and the complex floristic composition of the state. The combined number of specimens in the two largest collections in New Mexico is 158,000, compared with 425,000 specimens in the largest two collections in Arizona, 485,000 in Colorado and 1,272,000 in Texas (Holmgren et al., Index herbariorum part I: The herbaria of the world. 7th ed. 1981). The paucity of study specimens increases the probability that small local collections may well contain forms not found in the larger collections. This directory is compiled to inform students of New Mexico botany of the smaller, local collections available in the state.

Data for this list were collected from questionnaires mailed to 60 institutions including colleges and universities, national parks and monuments, national wildlife refuges, selected museums, and BLM district offices. Telephone calls were made to non-responders and a few herbaria were visited. From the results, 20 collections were judged appropriate for listing. Collections of less than 200 specimens, and those without data for specimens are not included. Six of the collections have Index Herbariorum standard acronyms; most of the rest probably will never be accessible in the Index. The data for the 20 collections are current as of December 1989. Although I am reasonably certain that this list is complete, I would appreciate hearing of other herbaria for inclusion in an updated list.

The largest collection, at the University of New Mexico, has 100,000 specimens. Next in size is New Mexico State University with 58,000 specimens. Eleven hold between 1000 and 15,000; seven contain less than 1000 specimens.

In 1888 the first herbarium in the state was established, at the State University of New Mexico at Las Cruces. It was the only collection in New Mexico until the 1920's, when the University of New Mexico, Cibola National Forest, and Carlsbad National Park set up herbaria.

Abbreviations used are: *No.* = number of specimens in the collection; *Spec.* = specializations of the collection; *Imp. coll.* = important collections and collectors; *Cur. res.* = current research at the herbarium.

### ALAMOGORDO

WHITE SANDS NATIONAL MONUMENT—P.O. Box 458, Alamogordo, 88310. (505) 479-6124. *Curator*: John A. Mangimeli. *No.*: 200. *Spec.*: Vascular plants of the White Sands National Monument.

### ALBUQUERQUE

BUREAU OF LAND MANAGEMENT—435 Montano NE, Albuquerque, 87107. (505) 761-4504. *Curator*: Dwain W. Vincent. *No.*: 570. *Spec.*: Compositae, Cactaceae, Leguminosae. *Imp. coll.*: *Sclerocactus mesaverdae*, *Pediocactus knowltonii*, *Sclerocactus whipplei*, *Pediocactus (Toumeyia) papyracantha*. *Cur. res.*: Range of *Abronia bigelovii* on the Todilto Formation, clearances for proposed gypsum mining.

CIBOLA NATIONAL FOREST HERBARIUM—10308 Candelaria NE, Albuquerque, 87112. (505) 275-5207. *Curator*: Fritz Winter. *No.*: 300. *Spec.*: Flora of the Cibola National Forest.



FOREST SERVICE HERBARIUM, SOUTHWESTERN REGION—USDA Forest Service, 517 Gold Avenue SW, Albuquerque, 87102. (505) 842-3228. *Curator*: Renee Galeano-Popp. *No.*: 10,000. *Spec.*: Flora of Arizona and New Mexico. *Imp. coll.*: Threatened and endangered species. *Cur. res.*: Status of rare species.

ROCKY MOUNTAIN FOREST AND RANGE EXPERIMENT STATION HERBARIUM (ALBU)—2205 Columbia SE, Albuquerque, 87106. (505) 766-2384. *Curator*: Deborah Hays. *No.*: 1368. *Imp. coll.*: Mountain grasslands collection, collected by Janet Williams, 1984.

UNIVERSITY OF NEW MEXICO HERBARIUM AND MUSEUM OF BOTANY (UNM)—Museum of Southwestern Biology, Department of Biology, University of New Mexico, Albuquerque, 87131. (505) 277-5330. *Curator*: Timothy Lowrey. *No.*: 100,000. *Spec.*: New Mexico and surrounding areas. *Imp. coll.*: Cacti—E. F. Castetter; Prince Pearce. Grasses—E. F. Castetter; W. C. Martin; R. Fletcher; L. D. Potter; W. Springfield. General collections—E. F. Castetter; H. Dittmer; L. D. Potter; W. C. Martin; R. Fletcher; P. Knight; C. R. Hutchins; Aven Nelson; Dunn and Lint; Los Medanos (WIPP). *Cur. res.*: Floristics of New Mexico; Ethnobotany; Biochemical Taxonomy; Distribution.

#### CARLSBAD

CARLSBAD CAVERNS NATIONAL PARK HERBARIUM—National Park Service, Drawer T, Carlsbad, 88220. (505) 885-8884. *Curator*: John E. Roth. *No.*: 700. *Spec.*: Guadalupe Mountains, including the large numbers of endemics located there. *Imp. coll.*: Prasil, 1952; Hewitt-McClelland, 1956; McCrary, 1952; Spangle, 1960. *Cur. res.*: Floristics list and coverage of species found within the Park's legal boundaries.

#### FARMINGTON

SAN JUAN COLLEGE HERBARIUM (NMSJ)—4601 College Blvd., Farmington, 87401. (505) 326-3311 ext 358. *Curator*: Kenneth D. Heil. *No.*: 12,000. *Spec.*: Four Corner Region, Baja Calif., Big Bend Region, TX, SE Utah; Colorado alpine. *Imp. coll.*: *Astragalus*, *Atriplex*, Cactaceae. *Cur. res.*: Cactaceae, *Eriogonum*, *Gilia*.

#### LAS CRUCES

BUREAU OF LAND MANAGEMENT HERBARIUM—1800 Marquess, Las Cruces, 88005. (505) 525-8228. *Curator*: Laird McIntosh. *No.*: 500. *Spec.*: Poaceae, *Astragalus*, Asteraceae. *Imp. coll.*: McIntosh, Sivinski, Spellenberg.

NEW MEXICO STATE UNIVERSITY HERBARIUM (NMC)—Biology Department, New Mexico State University, Las Cruces, 88003. (505) 646-3121. *Curator*: Richard Spellenberg. *No.*: 58,000. *Spec.*: New Mexico and northern Mexico. *Imp. coll.*: Wooton, Standley, Spellenberg. *Cur. res.*: Floristics of New Mexico and northern Mexico, systematics of Nyctaginaceae, *Astragalus*, Poaceae, *Quercus*.

RANGE SCIENCE HERBARIUM (NMCR)—Knox Hall, New Mexico State University, Las Cruces, 88003. (505) 646-1042. *Curator*: Kelly W. Allred. *No.*: 15,000. *Spec.*: Grasses of New Mexico, teaching specimens. *Cur. res.*: Grasses of New Mexico.

#### LAS VEGAS

NEW MEXICO HIGHLANDS UNIVERSITY HERBARIUM—Division of Science and Math, Las Vegas, 87701. (505) 425-7511, ext 264. *Curator*: Maureen Romine. *No.*: 1000. *Spec.*: Southwestern plants. *Imp. coll.*: Lora M. Shields. *Cur. res.*: Plants of north-eastern N.M.

#### LOS ALAMOS

BANDELIER NATIONAL MONUMENT HERBARIUM—Bandelier National Monument, Los Alamos, 87544. (505) 672-3861. *Curator*: Ken Stephens. *No.*: 2200. *Spec.*: Ref-



erence collection and vouchers to document the plant life of Bandelier. *Imp. coll.*: Clark (1941), Brian F. Jacobs (1986–88). *Cur. res.*: Plant inventory (1986–1988).

#### PORTALES

NATURAL HISTORY MUSEUM HERBARIUM—Eastern New Mexico University, Portales, 88130. (505) 562-2723. *Curator*: A. L. Gennaro. *No.*: 6000. *Spec.*: New Mexican Llano Estacado. *Imp. coll.*: David Yos, Mary Sublette, Jack Secor. *Cur. res.*: Llano Estacado.

#### SANTA FE

NEW MEXICO NATURAL HISTORY INSTITUTE HERBARIUM—St. John's College, Santa Fe, 87501-4599. (505) 982-3691. *Curator*: Roger S. Peterson. *No.*: 4500. *Spec.*: New Mexico, esp. Santa Fe, San Juan and Chaves counties; alpine tundra; *Astragalus* of AZ, NV, CA. *Cur. res.*: Ecological field projects involving NM alpine tundra, and Bitter Lake and Bosque del Apache National Wildlife Refuges.

SANTA FE NATIONAL FOREST HERBARIUM—USDA Forest Service, Piñon Building, 1220 St. Francis Blvd., Santa Fe, 87501. (505) 988-6961. *Curator*: Kathy Rinaldi. *No.*: 1500. *Spec.*: Grasses and forbs of the Santa Fe National Forest.

#### SILVER CITY

DEPARTMENT OF NATURAL SCIENCE HERBARIUM (SNM)—Western New Mexico University, Silver City, 88061. (505) 538-6423. *Curator*: Terry Heiner. *No.*: 6000. *Spec.*: Southwestern NM.

GILA NATIONAL FOREST HERBARIUM—USDA Forest Service, Silver City, 88061. (505) 388-8201. *Curator*: John Baldwin. *No.*: 700. *Spec.*: Local common species of grasses, forbs, and shrubs of southwestern NM, used primarily as a reference for plant identification.

#### SOCORRO

BOSQUE DEL APACHE NATIONAL WILDLIFE REFUGE HERBARIUM—Fish and Wildlife Service, P.O. Box 1246, Socorro, 87801. (505) 835-1828. *Curator*: John Taylor. *No.*: 500. *Spec.*: Plants collected from the Refuge. *Cur. res.*: Plant frequency and density; centers around alkaline areas.

BUREAU OF LAND MANAGEMENT, SOCORRO, HERBARIUM—198 Neel Ave., Socorro, 87801. (505) 835-0412. *Curator*: Wes Anderson. *No.*: 1848. *Spec.*: Plants of Socorro and Catron Counties. *Cur. res.*: Threatened and endangered plant inventories, in cooperation with The Nature Conservancy, on *Amsonia* and *Erigeron rhizomatus*. — CAROLYN DODSON, General Library, University of New Mexico, Albuquerque, NM 87131.

(Received 18 Mar 1988; revision accepted 25 Apr 1990.)



## REVIEW

*The Vascular Plants of Texas. A List, Updating the Manual of the Vascular Plants of Texas.* 2nd ed. MARSHALL C. JOHNSTON. iii + 107 pp., paperbound. 1990. Privately published. Copies may be obtained from Marshall C. Johnston, 3905 Avenue G, Austin, TX 78751 at \$14.00 (prepaid including tax and shipping) to North American addresses not requiring invoicing or billing, or \$17.00 (not prepaid) for shipments requiring invoicing or billing or for addresses outside North America. For Texas addresses add 7.75% sales tax.

This supplement is a much-needed updating and correction to the *Manual of the Vascular Plants of Texas* (Correll and Johnston 1969, Texas Research Foundation, Renner). Any flora is subject to modification and correction as knowledge accumulates. Many of the plants growing in Texas have been the subjects of taxonomic investigations during the past 20+ years. Reevaluations of taxonomic boundaries, discoveries of new taxa, nomenclatural changes, range extensions, and other products of taxonomic research gradually accumulate as a published flora gets older. Inevitably a scattering of typesetter's errors and errors of fact are discovered as well. One way of forestalling the need to completely redo a flora is to publish a supplement. This is the 2nd edition of the supplement; the first, which I have not seen, was issued in 1988.

One measure of the usefulness of a supplement is its integration with the original flora. Does the format of the supplement make it easy to use? In most respects the format of *The Vascular Plants of Texas* correlates well with the *Manual*. The pagination in the *Manual* is included in the supplement for each name, and the taxa are listed in the same sequence. The nature of each change from the *Manual* is indicated by an easily understood abbreviation or word (e.g., Corr. = correction of material in the *Manual*, Add, Dele., etc.). The supplement (with pages  $8\frac{1}{4} \times 10\frac{3}{4}$  inches) may not fit on the same library shelf as the *Manual* ( $6\frac{1}{4} \times 9\frac{1}{2}$  inches). The binding of the supplement is likely to come apart with more than occasional use.

Another measure of a supplement is completeness and accuracy of the information added to the flora. In a spot check I noted some problems here. Johnston has chosen to continue the use of *Eupatorium* (s.l.) over the segregate genera espoused by R. M. King and H. Robinson; this is a taxonomic decision. However, the supplement inexplicably includes in synonymy under *Eupatorium* some, but not all of the names in the segregate genera even though *The Genera of the Eupatorieae (Asteraceae)* (King and Robinson 1987, Missouri Bot. Gard. Monogr. Syst. Bot. 22) is a cited reference. Thus *Eupatoriadelphus fistulosus* (Barr.) King & Robins. is listed as a synonym of *Eupatorium fistulosum* Barr., but synonyms in *Ageratina* are not listed for *Eupatorium rothrockii* Gray, *E. herbaceum* (Gray) Greene, *E. havanense* H.B.K., and *E. wrightii* Gray. If a botanist prefers to use the segregate genera rather than the inclusive *Eupatorium* he or she would not be able to rely on the supplement.

Johnston's use of my work on *Pectis* is garbled. The wrong references are quoted for *P. angustifolia*, and I recognized three, not two varieties in Texas for this species; the widespread var. *angustifolia* was omitted from the supplement. My 1974 paper (Keil, Brittonia 26:30–36) was cited for *Pectis tenella*, which was not mentioned in the paper. *Pectis papposa* is represented in Texas by var. *grandis* Keil, published in the 1974 paper but omitted from the supplement. *Pectis filipes* is represented in Texas by var. *subnuda* Fern. (Keil, 1977, Rhodora 79:32–78), also omitted. *Pectis longipes* has not been documented from Texas (Keil letter to Johnston 1974). Finally, the pagination of the 1974 paper is incorrectly cited, and the name of sect. *Pectothrix*



was misspelled in the citation of the 1977 paper. I hope that the *Pectis* treatment is an isolated situation.

I will certainly use this reference. I think it a safe presumption that the greater part of the book is not tainted by the errors documented above. The extensive literature cited section is a compilation of references of use to any botanist carrying out floristic research in North America.—DAVID J. KEIL, Biological Sciences Department, California Polytechnic State University, San Luis Obispo, CA 93407.

## ANNOUNCEMENT

### NEW PUBLICATION

FERREN, W. R., JR., M. H. CAPELLI, A. PARIKH, D. L. MAGNEY, K. CLARK, AND J. R. HALLER. *Botanical Resources at Emma Wood State Beach and the Ventura River Estuary, California: Inventory and Management*. The Herbarium, Department of Biological Sciences, University of California, Santa Barbara, Environmental Report No. 15, 310 pp. 1990. Contents: physical environment, land use history, botanical resources, regulatory authorities and policies, management opportunities, potential interpretive themes, recommendations; Appendices: classification of wetlands, map of vegetation, map of marine macrophytes, map of invasive exotic species, quantitative vegetation analysis, annotated catalogue of marine algae, annotated catalogue of vascular plants. This is a comprehensive treatment of the botanical resources of an important coastal wetland ecosystem. Copies are available at \$20.00 from: Environmental Report Series, UCSB Herbarium, Department of Biological Sciences, University of California, Santa Barbara, CA 93106.



## EDITOR'S REPORT FOR VOLUME 37

This annual report provides an opportunity for the Editor to communicate the status of manuscripts received for publication in *Madroño* and to comment on other aspects of the journal. Between 1 July 1989 and 30 June 1990, 48 manuscripts were received (34 articles, 4 notes, and 10 noteworthy collections contributions totalling 20 individual taxa). Since 30 June 1990, 15 manuscripts have been received (9, 3, 3). The current status of the 36 unpublished manuscripts is 6 in review (5, 0, 1), 18 in revision (14, 1, 3), 1 note needing decision by the editor, and 11 accepted for publication (8, 3, 0). Volume 37 included 45 published manuscripts (27, 4, 9, 3 book reviews, and 1 memorial). The period between submittal and publication averaged 11–12 months for articles. Eight manuscripts (6, 1, 1) were rejected and one article was withdrawn. Six manuscripts (5, 0, 1) that were returned well over one year ago to the authors for revision are considered to have been withdrawn.

Several individuals have been of much help to me as Editor. I much appreciate the efforts of members of the Editorial Board. Steven Timbrook has once again prepared the annual Index and Table of Contents, and Rudolf Schmid has prepared announcements and reviews of new publications. I especially thank my wife, Kathy, for her patience, encouragement, and support.

My thanks also go to the authors whose papers I have edited for their patience and willingness to respond to my comments and those of the reviewers.

Without the support of Dr. Philip S. Bailey, Jr., Dean of the School of Science and Mathematics, and Dr. V. L. Holland, Chairman of the Biological Sciences Department at California Polytechnic State University, I could not have carried out my duties as Editor.

Articles and notes in *Madroño* continue to reflect the wide-ranging interests of members of the California Botanical Society. Topics discussed in volume 36 include cytology, ecology, floristics, history, hybridization, nomenclature, phytogeography, and systematics. The papers represent geographical areas from Canada, various areas of the United States, and Mexico. *Madroño* continues to serve as a source of additional information through reviews, commentaries, and announcements that inform members of the Society of publications, meetings, and other topics of interest. I encourage potential authors to continue to submit manuscripts that maintain the broad cross-section of botanical topics.

As I step down as Editor, I give a sigh of relief, but I look back fondly on the past three years as an unparalleled opportunity to learn about the interests and diversity of the botanical community. Through correspondence I have come to know a lot of you with whom I was not previously acquainted. Most heartening have been the comments from young authors whose initial efforts have been guided through to publication. I offer my encouragement and support to Dr. Jon E. Keeley, the incoming Editor.—D.J.K. 30 Nov 1990.



## REVIEWERS OF MANUSCRIPTS

As Editor, I thank all reviewers for their assistance with manuscripts. Special thanks are extended to those who reviewed several manuscripts published in 1990. I am very grateful to each reviewer for his or her generous contribution of time and effort. The quality of papers published in *Madroño* reflects this contribution. Reviewers for volume 37 are:

|                      |                       |                        |
|----------------------|-----------------------|------------------------|
| Isabella A. Abbott   | James R. Griffin      | Richard A. Pimentel    |
| Ihsan A. Al-Shehbaz  | Ronald L. Hartman     | Donald J. Pinkava      |
| Kelly W. Allred      | Douglas M. Henderson  | Robert A. Price        |
| Jim A. Bartel        | James Henrickson      | James S. Pringle       |
| Jerry M. Baskin      | B. M. Kapoor          | Charles F. Quibell     |
| R. Mitchel Beauchamp | Todd Keeler-Wolf      | John R. Reeder         |
| Mark Borchert        | Jon E. Keeley         | Rhonda Riggins         |
| Robert N. Bowman     | Walter A. Kelley      | Philip W. Rundel       |
| Mary Butterwick      | Lawrence M. Kelly     | Jerzy Rzedowski        |
| Kenton L. Chambers   | Arthur R. Kruckeberg  | William H. Schlesinger |
| Anita F. Cholewa     | Leslie R. Landrum     | J. Stephen Shelly      |
| Curtis Clark         | Meredith A. Lane      | James R. Shevock       |
| Susan G. Conard      | James M. Lenihan      | Paul A. Silva          |
| Daniel J. Crawford   | F. Harlan Lewis       | Dale M. Smith          |
| Arthur Cronquist     | Bruce E. Mahall       | James P. Smith         |
| Thomas F. Daniel     | William F. Mahler     | Shirley R. Sparling    |
| Roger del Moral      | Charles T. Mason      | Richard W. Spellenberg |
| Timothy A. Dickinson | Joy D. Mastrogiuseppe | John L. Strother       |
| Michael F. Doyle     | Malcolm G. McLeod     | Tod F. Stuessy         |
| James R. Ehleringer  | Dale W. McNeal, Jr.   | David Thompson         |
| Patrick E. Elvander  | Thomas J. Melchert    | Dale A. Thornburgh     |
| Joseph Ewan          | Rodney G. Myatt       | Robert F. Thorne       |
| Wayne R. Ferren, Jr. | Gerald B. Ownbey      | Joanna L. Tomassacci   |
| Christopher B. Field | Bruce D. Parfitt      | Billie L. Turner       |
| Leslie D. Gottlieb   | Duncan T. Patten      | Dieter H. Wilken       |

## DATES OF PUBLICATION OF MADROÑO, VOLUME 37

- Number 1, pages 1–68, published 1 March 1990
- Number 2, pages 69–148, published 25 April 1990
- Number 3, pages 149–224, published 18 September 1990
- Number 4, pages 225–321, published 7 February 1991



## INDEX TO VOLUME 37

Classified entries: major subjects, key words, and results; botanical names (new names are in **boldface**); geographical areas; reviews, commentaries. Incidental references to taxa (including most lists and tables) are not indexed separately. Species appearing in Noteworthy Collections are indexed under name, family, and state or country. Authors and titles are listed alphabetically by author in the Table of Contents to the volume.

*Abronia maritima*, stress tolerance, 200.

*Adenostoma fasciculatum*, growth dynamics with time after fire, 225.

Adiantaceae: (see *Notholaena*).

*Amblyolepis*, present status, 133.

*Ambrosia chamissonis*, stress tolerance, 200.

Anacardiaceae: (see *Malosma laurina*).

*Antennaria*: *A. media*, *A. pulchella*, and *A. scabra* of the Sierra Nevada and White Mountains, CA, systematic study, 171.

*Arabis dispar*, 62, and *A. pinzlae*, 64, noteworthy collections from CA.

*Arenaria nuttallii* subsp. *nuttallii* and *A. rubella* in Yellowstone National Park, WY, 214.

Arizona: Cannon, William Austin, the Sonoran Desert's first resident ecologist, 6; *Cirsium parryi* complex, 299; ***Cirsium parryi* subsp. mogollonicum**, new subsp., 300.

Noteworthy collections: *Asclepias cutleri*, 60; *Cathastecum erectum*, 216; *Dudleya pulverulenta* subsp. *arizonica*, *Eriogonum zionis* var. *zionis*, *Euphorbia eriantha*, *E. esula*, *Flaveria mcdougallii*, 61; *Leucocrinum montanum*, *Penstemon laevis*, 62; *Pisonia capitata*, 217.

Asclepiadaceae (see *Asclepias*).

*Asclepias cutleri*, noteworthy collection from AZ, 60.

Asteraceae: *Amblyolepis*, present status, 133; *Ambrosia chamissonis*, stress tolerance, 200; *Antennaria media*, *A. pulchella*, and *A. scabra* of the Sierra Nevada and White Mountains, CA, systematic study, 171; *Brickellia oblongifolia* var. *linifolia*, noteworthy collection from CA, 62; *Cirsium parryi* complex, 299; *Flaveria mcdougallii*, noteworthy collection from AZ, 61; *Haplopappus gilmanii*, noteworthy collection from CA, 63; *Raillardiaopsis*

*muirii*, systematic and biogeographic review, 43; *Senecio fuscatus*, *S. werneriifolius* and *Taraxacum eriophorum* in Yellowstone National Park, WY, 214; ***Viguiera* subg. Bahiopsis**, taxonomic revision, 149.

New taxa: ***Cirsium parryi* subsp. mogollonicum**, 300; ***Erigeron wilkenii***, 184; ***Thelesperma caespitosum***, 293; ***Viguiera* subg. Bahiopsis**, 155; ***V. carterae***, 157.

*Astragalus*, chromosome numbers for 15 taxa, 59.

Berberidaceae (see *Berberis*).

*Berberis*: ***B. muelleri***, 287, a new combination, and ***B. pimana***, 283, a new species, from northwestern Mexico.

Boraginaceae (see *Eritrichium*).

Brassicaceae: *Braya glabella* var. *glabella* in CO, 145; *Draba lonchocarpa* var. *lonchocarpa* in Yellowstone National Park, WY, 214; noteworthy collections from CA of *Arabis dispar*, 62, *A. pinzlae*, 64, *Draba monoensis*, 65, and *Phoenicaulis cheiranthoides*, 63.

*Braya glabella* var. *glabella* in CO, 145.

*Brickellia oblongifolia* var. *linifolia*, noteworthy collection from CA, 62.

California: *Abronia maritima*, *Ambrosia chamissonis*, and *Camissonia cheiranthifolia* stress tolerance, 200; *Antennaria media*, *A. pulchella*, and *A. scabra* of the Sierra Nevada and White Mountains, systematic study, 171; *Erythronium* in the Sierra Nevada, 261; forest associations of Little Lost Man Creek, Humboldt Co., old growth coastal redwood vegetation, 69; forest habitat types, South Warner Mountains, Modoc Co., 88; growth dynamics of two chaparral shrub species, *Adenostoma fasciculatum* and *Ceanothus*



- greggii*, with time after fire, 225; *Juglans californica*, demographic structure in woodlands, 237; *Leptodactylon californicum*, trichome pattern and geographic variation, 28; maritime stress tolerance of dune perennials, 200; *Raillardiopsis muirii*, systematic and biogeographic review, 43.
- New Taxa: *Clarkia concinna* subsp. **raichei**, 309; *Erythronium pluriflorum*, 268; *E. pusaterii*, 264; *Gentiana plurisetosa*, 289; *Leptodactylon californicum* subsp. **brevitrichomum**, 36; *L. c.* subsp. **leptotrichomum**, 38; *L. c.* subsp. **tomentosum**, 40; *Potentilla cristae*, 190; *Puccinellia howellii*, 55.
- Noteworthy collections: *Arabis dispar*, 62; *A. pinzlae*, 64; *Brickellia oblongifolia* var. *linifolia*, 62; *Carex incurviformis*, *C. norvegica*, 64; *Draba monoensis*, 65; *Haplopappus gilmanii*, *Hemitomes congestum*, *Lewisia disepala*, *L. kelloggii*, 63; *Malosma laurina*, 112; *Notholaena jonesii*, *Phoenicaulis cheiranthoides*, *Trautvetteria caroliniensis* var. *occidentalis*, 63.
- Caloglossa lepieurii*, noteworthy collection from Mexico, 236.
- Camissonia*: *C. cheiranthifolia*, stress tolerance, 200; *C. exilis*, noteworthy collection from UT, 62.
- Cannon, William Austin, the Sonoran Desert's first resident ecologist, 6.
- Carex*: *C. capitata*, *C. elynoides*, *C. haydeniana*, *C. obtusata*, and *C. pachystachya* in Yellowstone National Park, WY, 214; *C. incurviformis* and *C. norvegica*, noteworthy collections from CA, 64.
- Caryophyllaceae: *Arenaria nuttallii* subsp. *nuttallii*, *A. rubella*, *Cerastium beeringianum* var. *capillare*, *Silene hitchguirei*, and *Stellaria monantha* in Yellowstone National Park, WY, 214.
- Cathestecum erectum*, noteworthy collection from AZ, 216.
- Ceanothus greggii*, growth dynamics with time after fire, 225.
- Cerastium beeringianum* var. *capillare* in Yellowstone National Park, WY, 214.
- Chandonanthus hirtellus*, noteworthy collection from Mexico, 217.
- Chaparral, growth dynamics of two shrub species, *Adenostoma fasciculatum* and *Ceanothus greggii*, with time after fire, 225.
- Chloris verticillata*, noteworthy collection from WY, 140.
- Chromosome counts: *Amblyolepis setigera*, 135; *Astragalus*, 15 taxa, 59; *Clarkia concinna* subsp. **raichei**, 309; *Crataegus douglasii* and *C. suksdorfii*, 277; *Mimulus glabratus* complex, 143; *Potentilla cristae*, 190; *Raillardiopsis muirii* and *R. scabrida*, 47.
- Cirsium*: *C. parryi* complex, 299; *C. p.* subsp. **mogollonicum**, new subsp. from AZ, 300.
- Clarkia concinna* subsp. **raichei**, a new subsp. from CA, 309.
- Colorado: *Braya glabella* var. *glabella* in, 145; review of *Rare Plants of Colorado*, 147.
- New taxa: *Erigeron wilkenii*, 184; *Pentstemon fremontii* var. **glabrescens**, 195.
- Compositae (see Asteraceae).
- Convolvulaceae: Comments on southwestern United States *Evolvulus* and *Ipomoea*, 124.
- Crassulaceae (see *Dudleya*).
- Crataegus suksdorfii*, specific status, 274.
- Critchfield, William Burke, memorial, 221.
- Cruciferae (see Brassicaceae).
- Cyperaceae (see *Carex*).
- Delesseriaceae (see *Caloglossa*).
- Draba lonchocarpa* var. *lonchocarpa* in Yellowstone National Park, WY, 214; *D. monoensis*, noteworthy collection from CA, 65.
- Dune perennials, maritime stress tolerance of, 200.
- Dudleya pulverulenta* subsp. *arizonica*, noteworthy collection from AZ, 61.
- Ericaceae (see *Hemitomes*).
- Erigeron wilkenii*, new species from CO, 184.
- Eritrichium nanum* in Yellowstone National Park, WY, 214.
- Erythronium* in the Sierra Nevada, CA, 261; *E. pluriflorum*, 268, new species; *E. pusaterii*, 264, new combination.
- Euphorbia eriantha* and *E. esula*, noteworthy collections from AZ, 61.
- Euphorbiaceae (see *Euphorbia*).
- Evolvulus* and *Ipomoea*, in southwestern United States, 124.



Fabaceae (see *Astragalus*).

*Festuca baffinensis* in Yellowstone National Park, WY, 214.

Fire influence on growth dynamics of two chaparral shrub species, 225.

Forest associations of Little Lost Man Creek, Humboldt Co., CA, old growth coastal redwood vegetation, 69.

Forest habitat types, South Warner Mountains, Modoc Co., CA, 88.

**Gentiana plurisetosa**, new species from northern CA and southern OR, 289.

Gentianaceae (see *Gentiana* and *Gentianella*).

*Gentianella tenella* in Yellowstone National Park, WY, 214.

Gramineae (see Poaceae).

*Haplopappus gilmanii*, noteworthy collection from CA, 63.

*Hemitomes congestum*, noteworthy collection from CA, 63.

Herbaria of New Mexico, 311.

*Heribaudiella fluviatilis*, noteworthy collection from WA, 144.

Hookeriaceae (see *Rhynchostegiopsis*).

Hypnaceae (see *Hypnum*).

*Hypnum vaucherii*, noteworthy collection from Mexico, 217.

*Ipomoea* and *Evolvulus*, in southwestern United States, 124.

Iridaceae (see *Iris*).

*Iris thompsonii*, taxonomic status, 113.

Juglandaceae (see *Juglans*).

*Juglans californica*, demographic structure in woodlands of southern California, 237.

Jungermanniaceae (see *Chandonanthus*).

Leguminosae (see Fabaceae).

Lejeuneaceae (see *Omphalanthus*).

*Leptodactylon californicum*: trichome pattern and geographic variation, 28; new taxa: *L. c.* subsp. **brevitrichomum**, 36; *L. c.* subsp. **leptotrichomum**, 38; *L. c.* subsp. **tomentosum**, 40.

*Leucocrinum montanum*, noteworthy collection from AZ, 62.

*Lewisia disepala* and *L. kelloggii*, noteworthy collections from CA, 63.

Liliaceae: *Erythronium* in the Sierra Nevada, CA, 261; *E. pluriflorum*, 268, new species; *E. pusaterii*, 264, new com-

bination; *Leucocrinum montanum*, noteworthy collection from AZ, 62; *Lloydia serotina* in Yellowstone National Park, WY, 214.

Lithodermataceae (see *Heribaudiella*).

Little Lost Man Creek, Humboldt Co., CA, forest associations in old growth coastal redwood vegetation, 69.

*Lloydia serotina* in Yellowstone National Park, WY, 214.

*Malosma laurina*, noteworthy collection from CA, 112.

Memorial to William Burke Critchfield, 221.

Mexico: genetic uniformity of El Arbol del Tule, *Taxodium mucronatum*, near Oaxaca, Mexico, 1; **Viguiera** subg. **Bahiopsis**, taxonomic revision, 149.

New taxa: **Berberis muelleri**, 287; **B. pimana**, 283; **Viguiera** subg. **Bahiopsis**, 155; *V. carterae*, 157.

Noteworthy collections: *Caloglossa leprieurii*, 236; *Chandonanthus hirtellus*, *Hypnum vaucherii*, *Omphalanthus wallisii*, and *Rhynchostegiopsis planifolia*, 217.

*Mimulus glabratus* complex, chromosome counts, 141.

New Mexico, herbaria, 311.

*Notholaena jonesii*, noteworthy collection from CA, 63.

Nyctaginaceae: *Abronia maritima*, stress tolerance, 200; *Pisonia capitata*, noteworthy collection from AZ, 217.

*Oemleria cerasiformis*, habitat relationships, 249.

*Omphalanthus wallisii*, noteworthy collection from Mexico, 218.

Onagraceae (see *Camissonia* and *Clarkia*).

Oregon: **Gentiana plurisetosa**, new species, 289.

**Penstemon fremontii** var. **glabrescens**, new variety from CO, 195; *P. laevis*, noteworthy collection from AZ, 62.

*Pisonia capitata*, noteworthy collection from AZ, 217.

*Poa secunda* var. *incurva* in Yellowstone National Park, WY, 214.

Poaceae: *Cathastecum erectum*, noteworthy collection from AZ, 216; *Chloris verticillata*, noteworthy collection from



- WY, 140; *Festuca baffinensis* and *Poa secunda* var. *incurva* in Yellowstone National Park, WY, 214; **Puccinellia howellii**, a new species from CA, 55.
- Polemoniaceae (see *Leptodactylon*).
- Polygonaceae (see *Eriogonum*).
- Portulacaceae (see *Lewisia*).
- Potentilla*: **P. cristae**, new species from northwestern CA, 190; *P. nivea* in Yellowstone National Park, WY, 214.
- Puccinellia howellii**, a new species from CA, 55.
- Raillardella* (see *Raillardiopsis*).
- Raillardiopsis muirii*, systematic and biogeographic review, 43.
- Ranunculaceae (see *Trautvetteria*).
- Reviews: Rupert C. Barneby, *Intermountain Flora: Vascular Plants of the Intermountain West, U.S.A.*, Volume 3, Part B, 219; The Colorado Native Plant Society, *Rare Plants of Colorado*, 147; Marshall C. Johnston, *The Vascular Plants of Texas. A List, Updating the Manual of the Vascular Plants of Texas*. 2nd ed., 314.
- Rhamnaceae (see *Ceanothus*).
- Rhynchostegiopsis planifolia*, noteworthy collection from Mexico, 217.
- Rosaceae: *Adenostoma fasciculatum*, growth dynamics with time after fire, 225; *Crataegus suksdorfii*, specific status, 274; *Oemleria cerasiformis*, habitat relationships, 249; **Potentilla cristae**, new species from northwestern CA, 190; *P. nivea* in Yellowstone National Park, WY, 214.
- Santa Lucia Range, CA: *Raillardiopsis muirii*, systematic and biogeographic review, 43.
- Saxifraga adscendens* var. *oregonensis*, *S. flagellaris* var. *crandallii*, and *S. rivularis* subsp. *rivularis* var. *flexuosa* in Yellowstone National Park, WY, 214.
- Saxifragaceae (see *Saxifraga*).
- Scrophulariaceae: *Mimulus glabratus* complex, chromosome counts, 141; **Penstemon fremontii** var. *glabrescens*, new variety from CO, 195; *P. laevis*, noteworthy collection from AZ, 62.
- Senecio*: *S. fuscatus* and *S. werneriiifolius* in Yellowstone National Park, WY, 214.
- Sequoia sempervirens*: forest associations of Little Lost Man Creek, Humboldt Co., CA, old growth coastal redwood vegetation, 69.
- Sierra Nevada range, CA: (see *Antennaria* and *Erythronium*).
- Silene hitchguirei* in Yellowstone National Park, WY, 214.
- Sonoran Desert, William Austin Cannon, first resident ecologist, 6.
- South Warner Mountains, Modoc Co., CA, forest habitat types, 88.
- Stress tolerance, maritime dune perennials, 200.
- Taraxacum eriophorum* in Yellowstone National Park, WY, 214.
- Taxodiaceae (see *Sequoia* and *Taxodium*).
- Taxodium mucronatum*, genetic uniformity of El Arbol del Tule, near Oaxaca, Mexico, 1.
- Thelesperma caespitosum**, new species from UT and WY, 293.
- Trautvetteria caroliniensis* var. *occidentalis*, noteworthy collection from CA, 63.
- Trinity Mountains, CA: **Puccinellia howellii**, 55.
- Utah: *Camissonia exilis*, noteworthy collection, 62; **Thelesperma caespitosum**, new species, 293.
- Viguiera** subg. **Bahiopsis**, taxonomic revision, 149, **V. carterae**, new species from Mexico, 157.
- Washington: Noteworthy collection of *Heribaudiella fluviatilis*, 144.
- White Mountains, CA: (see *Antennaria*).
- Woodlands, demographic structure of *Juglans californica* in, 237.
- Wyoming (see also Yellowstone National Park): *Chloris verticillata*, noteworthy collection, 140; **Thelesperma caespitosum**, new species, 293.
- Yellowstone National Park, WY, additions to vascular flora, 214.







## SUBSCRIPTIONS—MEMBERSHIP

Membership in the California Botanical Society is open to individuals (\$22 per year; students \$12 per year for a maximum of seven years). Members of the Society receive MADROÑO free. Family memberships (\$25) include one five-page publishing allotment and one journal. Emeritus rates are available from the Corresponding Secretary. Institutional subscriptions to MADROÑO are available (\$50). Membership is based on a calendar year only. Applications for membership (including dues), orders for subscriptions, and renewal payments should be sent to the Treasurer. Requests and rates for back issues, changes of address, and undelivered copies of MADROÑO should be sent to the Corresponding Secretary.

## INFORMATION FOR CONTRIBUTORS

Manuscripts submitted for publication in MADROÑO should be sent to the editor. All authors must be members, and membership is prerequisite for review.

Manuscripts may be submitted in English or Spanish. English-language manuscripts dealing with taxa or topics of Latin America and Spanish-language manuscripts must have a Spanish RESUMEN and an English ABSTRACT.

Manuscripts and review copies of illustrations must be submitted in triplicate for all articles and short items (NOTES, NOTEWORTHY COLLECTIONS, POINTS OF VIEW, etc.). Follow the format used in recent issues for the type of item submitted. Allow ample margins all around. Manuscripts MUST BE DOUBLE SPACED THROUGHOUT. For articles this includes title (all caps, centered), author names (all caps, centered), addresses (caps and lower case, centered), abstract and resumen, text, acknowledgments, literature cited, tables (caption on same page), and figure captions (grouped as consecutive paragraphs on one page). Order parts in the sequence listed, ending with figures. Each page should have a running header that includes the name(s) of the author(s), a shortened title, and the page number. Do not use a separate cover page or “erasable” paper. Avoid footnotes except to indicate address changes. Table and figure captions should contain all information relevant to information presented. All measurements and elevations should be in metric units. Specimen citations may include English or metric distance measurements.

Line copy illustrations should be clean and legible, proportioned (including captions) to the MADROÑO page, and designed for reduction to  $\frac{2}{3}$  original size. Scales should be included in figures, as should explanation of symbols, including graph coordinates. Symbols smaller than 1 mm after reduction are not acceptable. Maps must include latitude and longitude references. Halftone copy should be designed for reproduction at actual size. In no case should original illustrations be sent prior to the acceptance of a manuscript. When needed they should be mounted on stiff cardboard and sent flat. No illustrations larger than 22 × 28 cm will be accepted.

Presentation of nomenclatural matter (accepted names, synonyms, typification) should follow the format used for members of the *Allium sanbornii* complex in MADROÑO 36:124–128. 1989. Institutional abbreviations in specimen citations should follow Holmgren, Keuken, and Schofield, *Index Herbariorum*, 7th ed. Names of authors of scientific names should be abbreviated according to the Kew *Draft Index of Author Abbreviations* (1980). Abbreviation of serial titles should be those in *Botanico-Periodicum-Huntianum* (Lawrence et al., 1968, Hunt Botanical Library, Pittsburgh). If the correct abbreviation cannot be determined, the full serial title should be used. Titles of books should be given in full, together with the place and date of publication, publisher, and edition, if other than the first.

All members of the California Botanical Society are allotted five free pages per volume in MADROÑO. Joint authors may split the full page number. Beyond that number of pages a required editorial fee of \$65.00 per page will be assessed. The purpose of this fee is not to pay directly for the costs of publishing any particular paper, but rather to allow the Society to continue publishing MADROÑO on a reasonable schedule, with equity among all members for access to its pages. Printer's fees for illustrations and typographically difficult material @ \$35.00 per page (if their sum exceeds 30 percent of the paper) and for author's changes after typesetting @ \$4.50 per line will be charged to authors.

At the time of submission, authors must provide information describing the extent to which data in the manuscript have been used in other papers that are published, in press, submitted, or soon to be submitted elsewhere.



|  |          |
|--|----------|
| AWARDS FOR BEST PAPERS                         | 273      |
| NEW PUBLICATIONS                               | 260, 315 |
| CHANGE IN SUBSCRIPTION RATE FOR MADROÑO        | 248      |
| INTERNATIONAL CONFERENCE ON SERPENTINE ECOLOGY | 288      |
| COMMENTARY                                     |          |
| EDITOR'S REPORT FOR VOLUME 37                  | 316      |
| REVIEWERS OF MANUSCRIPTS                       | 317      |
| INDEX TO VOLUME 37                             | 318      |
| DEDICATION                                     | ii       |
| TABLE OF CONTENTS FOR VOLUME 37                | iv       |
| DATES OF PUBLICATION                           | 317      |



CALIFORNIA BOTANICAL SOCIETY















SMITHSONIAN INSTITUTION LIBRARIES



3 9088 01111 8213